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CONTENTS

PAGE

ORIGINAL PAPERS

Bassindale, R. Studies on the Biology of the Bristol Channel. XI. The Physical Environment and Intertidal Fauna of the Southern Shores of the Bristol Channel and Severn Estuary. (With ten Figures in the Text) 1

Chu, S. P. The Influence of the Mineral Composition of the Medium on the Growth of Planktonic Algae. Part II. The Influence of the Concentration of Inorganic Nitrogen and Phosphate Phosphorus. (With fifteen Figures in the Text) . . 109

David, Harold M. Studies in the Autecology of *Ascophyllum nodosum* Le Jol. (With Plate 12 and five Figures in the Text) 178

Godwin, H. Coastal Peat Beds of the British Isles and North Sea. Presidential Address to the British Ecological Society 1943. (With twenty-four Figures in the Text) 199

Hepburn, Ian. A Study of the Vegetation of Sea-Cliffs in North Cornwall. (With Plates 1, 2 and one Figure in the Text) 30

Thomas, A. S. The Vegetation of the Karamoja District, Uganda. An Illustration of Biological Factors in Tropical Ecology. (With Plates 3–11 and one Figure in the Text) 149

REVIEWS

Journal of Animal Ecology (Vol. 11, No. 2) 40

The Mycorrhizal Relations of Pinus 41

The Reproductive Capacity of Plants 44

The Journal of Animal Ecology (Vol. 12, No. 1) 248

Some ecological aspects of afforestation and forestry in Britain 248

John Ray, Naturalist 249

BIOLOGICAL FLORA OF THE BRITISH ISLES

Accounts Published or in Preparation 48

Juncus macer S. F. Gray by P. W. Richards 51

Juncus filiformis L. by P. W. Richards 60

Rhamnus cathartica L. by H. Godwin 66

Frangula alnus Miller by H. Godwin 77

BRITISH ECOLOGICAL SOCIETY

Memorandum on Nomenclature and Taxonomy in the Biological Flora 93

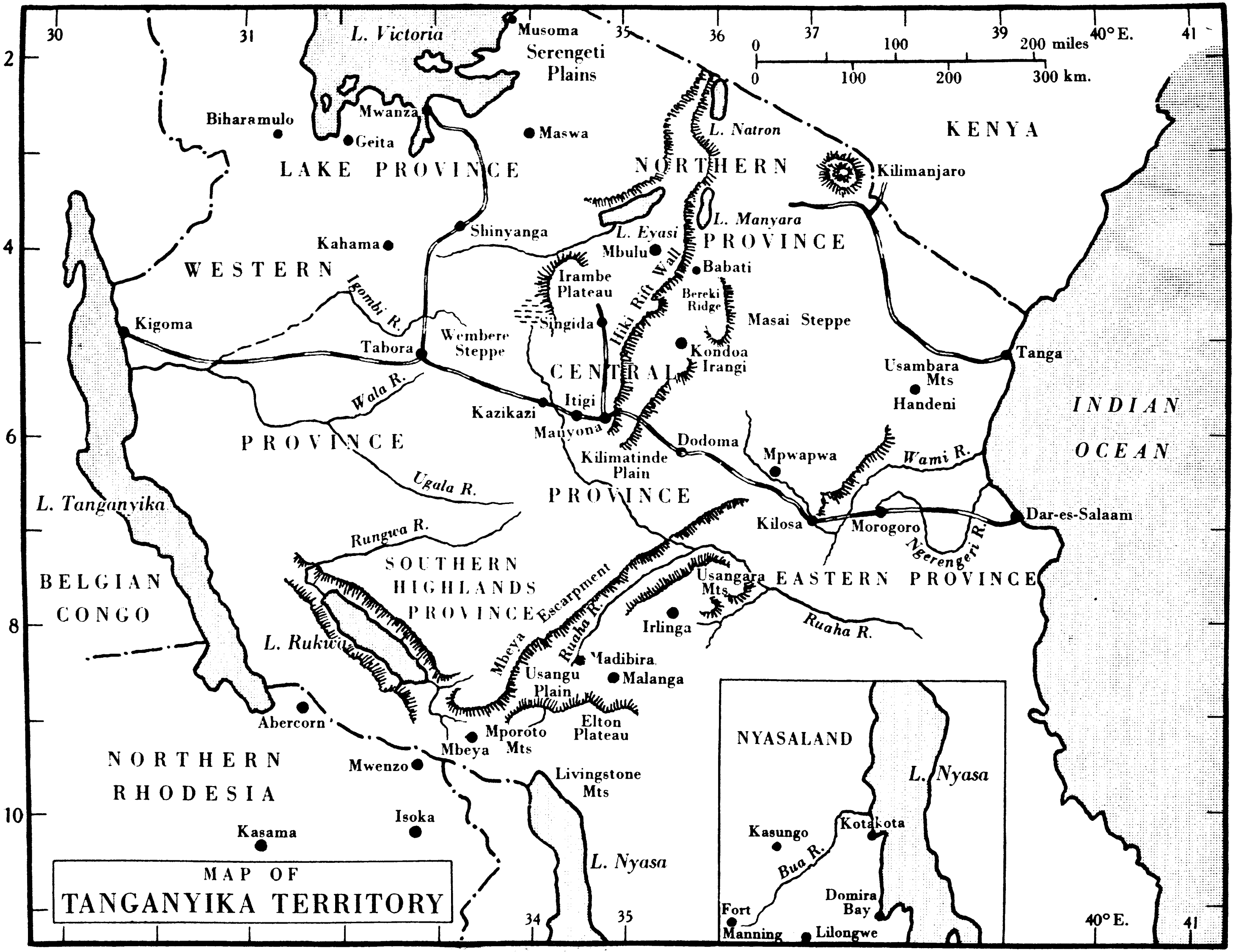
Annual Meeting in the University Botany School, Cambridge 97

List of Members 100

ERRATA 250

RUSSIAN-ENGLISH TECHNICAL GLOSSARIES 251

B. D. BURTT



MAP OF
TANGANYIKA TERRITORY

Burtt Memorial Supplement

Imperial Agricultural Research Institute, New Delhi

VOLUME 31, NO. 1 17 MAY 1943

STUDIES ON THE BIOLOGY OF THE BRISTOL CHANNEL

XI. THE PHYSICAL ENVIRONMENT AND INTERTIDAL FAUNA OF THE SOUTHERN SHORES OF THE BRISTOL CHANNEL AND SEVERN ESTUARY

BY R. BASSINDALE, *Department of Zoology, University of Bristol*

(*With ten Figures in the Text*)

CONTENTS

	PAGE
INTRODUCTION	1
PHYSICAL DATA	2
General description of the estuary	2
The tides	3
The silt content of estuary water	8
Salinity data	14
Other physical data	21
BIOLOGICAL DATA	21
The flora	21
The general fauna	22
Seasonal changes	26
Other faunistic notes	26
SUMMARY	27
REFERENCES	29

INTRODUCTION

The fisheries of the southern shores of the Bristol Channel and Severn Estuary have been the subject of much investigation (see Lloyd, 1940, 1942; Matthews, 1942). The intertidal invertebrate fauna, on the other hand, had only been studied in detail at Ilfracombe. Recently, contributions from the Bristol University Zoology Department on the Biology of the Bristol Channel have described the invertebrate fauna of the shores of Steepholm and Portishead (Yonge & Lloyd, 1938; Purchon, 1937) and of Portishead Dock (Purchon, 1937, 1939). Matthews has also contributed papers on Denny Island and the fauna around Weston (Matthews, 1923, 1932). There remained, therefore, a large gap in our knowledge of the invertebrate fauna, and the present paper describes an investigation of the fauna and physical features of the estuary from above Gloucester to Ilfracombe. During 1939 and 1940 selected collecting stations were visited and the fauna recorded. Previous accounts were also investigated, and the information assembled has been published in the form of a fauna list (Bassindale, 1940). Information on the physical conditions will be presented here.

Acknowledgements of assistance received during the survey were made in the previous publication. For additional assistance I am indebted to the following: the Admiralty for access to records and permission to publish some of the data provided; Drs A. Parker and B. A. Southgate for assistance in connexion with the Admiralty data; Profs. A. M. Tyndall, H. R. Hassé, W. F. Whittard and A. H. Gibson, Dr A. T. Doodson, Commander J. R. Lumby and Dr Carruthers for information and references each in his own subject; and Lieut. Wide, Capt. W. Groves and Mr W. Hayward for assistance in sampling. The work and preparation of the paper have been under the general supervision of Prof. C. M. Yonge and expenses have been defrayed by the Leverhulme Trustees, the Challenger Society and the Colston Research Society of the University of Bristol.

PHYSICAL DATA

General description of the estuary

The Bristol Channel and Severn Estuary form a long, gradually tapering waterway up which the tidal wave travels with ever-increasing momentum until it forms, during spring tides, the spectacular bore for which the Severn is famous. The exceptional range of tide produced by this same gradual tapering of the channel is also well known. Correlated with the extreme range of tide are the unusually rapid and turbulent currents which keep in suspension a very large amount of silt.

The hydrography of the Severn has been extensively investigated. Consequently it has been possible to draw on a large body of information. The major works cited are the *Reports of the Severn Barrage Committee of the Economic Advisory Council*. This Committee investigated the possibility of building a barrage to convert tidal into electric energy, and it collected much tidal and geographical data.

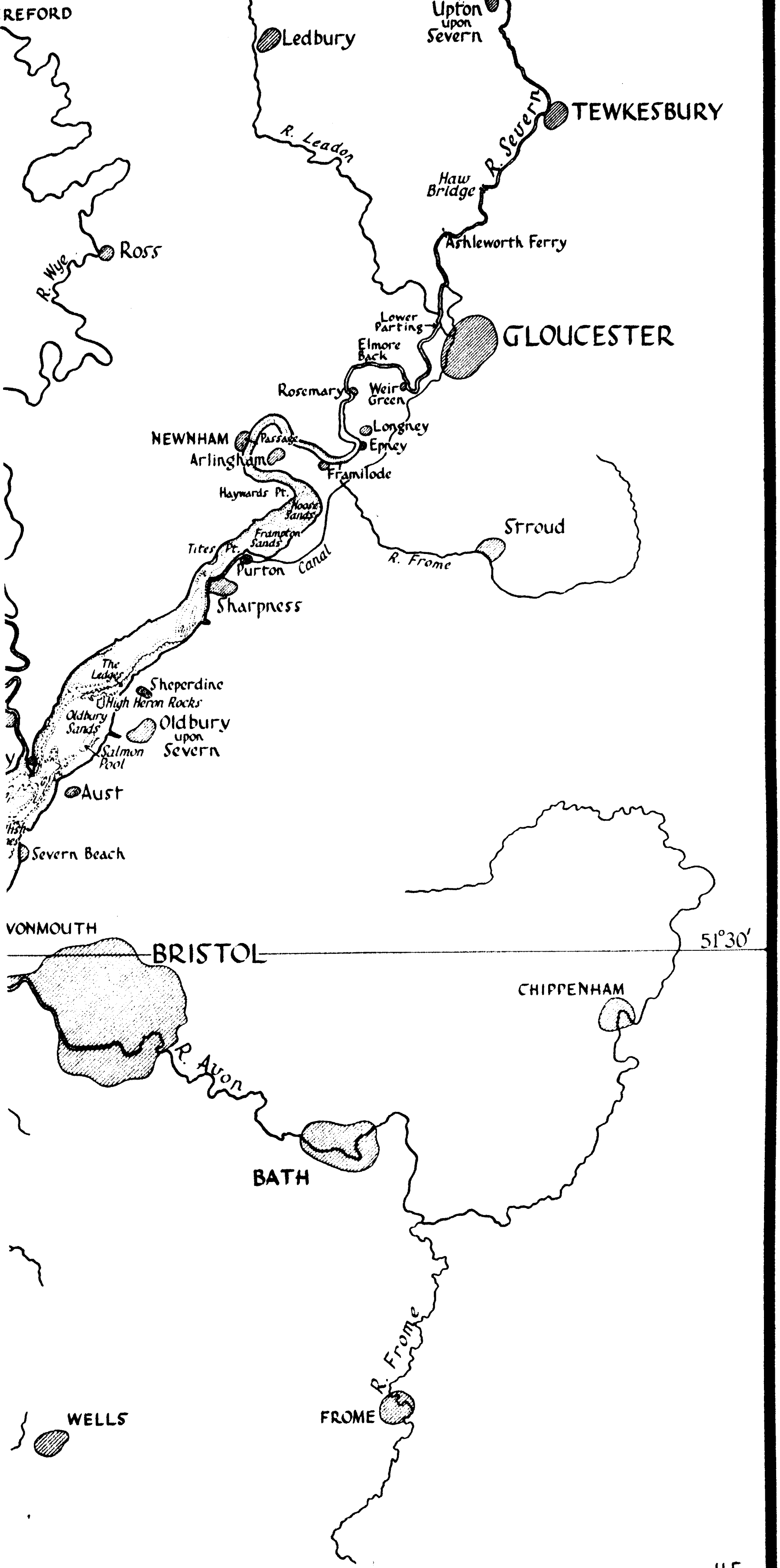
The Severn drains a catchment area of 4350 sq. miles and, to its junction at King Road (Avonmouth) with the Bristol Channel, it is 220 miles long. The Bristol Channel runs from King Road to Morte Point (for the purposes of this survey)—a distance of 70 miles.

The highest point at which tidal effects may be observed during spring tides is Upton-upon-Severn, about 66 miles from King Road. From Upton to Gloucester the estuary presents the normal appearance of a large river. From Gloucester to Epney the range of tide is greater, and although the estuary is still narrow the steep earth banks bear witness to the tidal nature of this section. 'After the large loop of 9 miles below Epney the estuary widens to form a basin 1¼ miles wide containing the Noose and Frampton Sands. It then narrows to about ½ mile at Sharpness, afterwards gradually widening to 2¼ miles at the Oldbury Sands. At Aust the shores converge to give a passage about ¾ mile wide, opening out again above the English Stones (Severn Beach) to a width of 2·3 miles. The low-water channel is here very narrow and deep and is called the Shoots. Below the English Stones the estuary widens to 5·4 miles at Avonmouth, 8·4 miles at Newport and 9·2 miles at Cardiff' (Gibson, 1933).

In general, mud banks line the shore and sand banks occur in the middle of the estuary. The mud banks are frequently extensive and are found from Tites Point to Blue Anchor Bay.

The sand banks of the estuary tend to be connected to the shore (usually by way of a mud bank), but in the upper Bristol Channel island banks occur as well as shore banks. This distribution conforms with that found in the Mersey Estuary and is a function of the current system (Southgate *et al.* 1938).

Much rock is exposed in all parts of the estuary, and collecting stations have been chosen at rocky places. A description of the collecting stations has been given elsewhere (Bassindale, 1942*a*). Stated briefly, exposures of rock or shingle occur at Sheperdine, Aust, the English Stones, Portishead, Kilve and Blue Anchor. Shingle appears extensively at Blue Anchor (west end) and Minehead, and from this point the coast consists of steep cliffs and the foreshore is mainly narrow and of rock or shingle with only occasional patches of sand. The rocks exposed in the estuary are mainly Triassic sandstones and marls with some limestone. In the upper Bristol Channel there is little sandstone or marl, but


REFORD
Ledbury
Upton upon Severn
TEWKESBURY
R. Severn
R. Leadon
Haw Bridge
Ashleworth Ferry
Ross
R. Wye
Lower Parting
GLOUCESTER
Elmore Back
Rosemary
Weir Green
Longney
Epney
NEWNHAM
Passage
Arlingham
Framilode
Haywards Pt.
Noose Sands
Frampton Sands
Tites Pt.
Purton
Canal
Stroud
R. Frome
Sharpness
The Ledges
Sheperdine
High Herom Rocks
Oldbury Sands
Oldbury upon Severn
Salmon Pool
Aust
Severn Beach
VONMOUTH
BRISTOL
51°30′
CHIPPENHAM
R. Avon
BATH
R. Frome
FROME
WELLS

limestone is common and shales appear at Kilve and Blue Anchor. Devonian rocks extend from Porlock Weir westward, and begin at Porlock Weir with grits and shales.

On the map (Fig. 1) the collecting stations and estuarine banks are shown. The distances used in this paper are shown elsewhere, on a sketch map (Bassindale, 1942*a*). The distances have been measured by opisometer along the winding low-water channel to Blue Anchor and then due west to Morte Point. They are expressed in miles from King Road near Avonmouth—which is the seaward limit of the Severn Estuary.

Ports on the Bristol Channel and Severn Estuary are served by ocean-going ships. The largest vessels can use the docks at Swansea, Barry, Cardiff, Newport, Portishead and Avonmouth, while ships of 4000 tons can ascend the estuary to the docks at Sharpness. From here vessels of up to 190 ft. in length can use the Berkeley and Gloucester ship canal to reach Gloucester (the river between Sharpness and Gloucester being treacherous), and the canalization of the Severn from Gloucester to Stourport permits vessels of 250 tons to reach Worcester and of 110 tons to reach Stourport.

Large tributaries join the estuary and upper Bristol Channel at Chepstow (the Wye), Newport (the Usk), Avonmouth (the Avon) and Bridgwater (the Parrett). The catchment areas of these four rivers are respectively 890, 1610, 540 and 560 sq. miles compared to the Severn's 4350 sq. miles. The average flow of the Severn is given as 4270 cusecs (cubic ft. per sec.) and of the Wye 2000, the Usk 670, the Avon 980 and the Parrett 670 cusecs.

The tides

Atlantic tides in general, and consequently the tidal waves affecting the Bristol Channel, are semi-diurnal and show little diurnal inequality. There are the usual periods of spring tides and neap tides succeeding each other at weekly intervals. The source of the sea water entering the Bristol Channel on the flood tide is of interest, and the current system involved has been described by Matthews (1913). The tide wave approaches the Bristol Channel from the south-west and enters the Irish Sea and English Channel, producing high water in these two areas.

> At high water at Liverpool Bay there is slack water over nearly the whole of the North Channel and Irish Sea, though weak shore streams are perceptible. In the St George's Channel the ebb has already begun to flow southwards, and in the Bristol Channel it is just ending; that is, the ebb of the Irish Sea coincides with the flood of the Bristol Channel.
>
> As the water falls at Liverpool Bay it ebbs northwards through the North Channel and southwards through the St George's Channel. The latter part divides into two branches; the easterly one flows round the south-west coast of Wales to form the flood tide of the northern half of the Bristol Channel, and at the same time the ebb of the English Channel turns to the north-east round Land's End and flows along the north coasts of Cornwall and Devon to become the flood tide of the southern half of the Bristol Channel. Shortly, *the flood of the Bristol Channel coincides with and is in great part derived from the ebb tides of the English Channel on one side and St George's Channel on the other*...the ebb continues until low water at Liverpool Bay, when again there is slack water over the whole area north of the latitude of the Tuskar, neglecting as before the weak coastal streams. In the Bristol Channel, and in its southern half in particular, the last of the flood is still running.
>
> As the water rises at Liverpool Bay the ebb sets out of the Bristol Channel, south-westwards towards Land's End, and westward and north-westwards into the St George's Channel, where the flood is now running....
>
> The Irish Channel contains two areas where the stream is almost imperceptible and where the power of the tide to cause vertical mixing of the water is almost *nil*. One of these, to the westward of the Isle of Man, has already been mentioned. The other lies off the entrance to the Bristol Channel. Its

position changes slightly with the state of the tide, the centre moving from about 51 N. lat. and 6 W. long. to a point not far from the opposite coast of Ireland. In both these areas we find a bottom consisting largely of mud which is able to deposit here owing to the small scour and...the relatively undisturbed state of the water is particularly favourable to the formation of horizontal layers of different salinities and temperatures. (Matthews, 1913, pp. 9–10.)

Matthews then goes on to show that there is a cyclonic (anticlockwise) movement of the water around this slack area and that the most saline and warmest water is derived from the current which enters the Bristol Channel area from the English Channel between the Scilly Islands and Lands End. This current, whose axis of highest salinity is only a few miles off Lands End, gives rise to the cyclonic circulation and 'leads to some rather unusual physical conditions such for instance as the fact that as we travel seawards from the N.W. Cornish coast the salinity begins to fall at a comparatively short distance from the shore and may reach its lowest value in mid-channel' (p. 21).

Although of considerable interest from the point of view of oceanic biologists it must be mentioned that these 'high' and 'low' salinities are variations from just above to just below 35 g./l. None the less, it is obvious that the southern shores of the Bristol Channel draw their salt water on the flood from oceanic sources rather than from the slightly diluted water from the Irish Sea as occurs on the northern shores. How far the influence of this warm and saline water extends obviously depends on the currents in the upper Bristol Channel. Owing to the bend of the Channel at Weston the ebb currents of the estuary seem to be directed against the southern shores in the region of Kilve and Blue Anchor. If, as may be the case, the ebb current swings offshore westward of Blue Anchor, then the proposed extension of the present survey to Porlock and Ilfracombe may lead to the discovery of unusual species living under the influence of the water from the English Channel. It is well known that the fauna of Ilfracombe is rich, and some interesting species have already been found on the shore at Stolford and Kilve (*Solaster papposus*, *Pasiphae sivado*, *Leptocephalus* larvae of the Conger eel, *Hippocampus* and *Maurolicus muelleri*).

The progressive tidal wave which sweeps up the Bristol Channel is subject to frictional forces which cause the level of the wave crest (i.e. the height of high water) to be raised and the level of the foot or trough (i.e. the height of low water) to be lowered (Fig. 2). (A mathematical analysis of this phenomenon, a discussion of previous theories and a list of useful references is given by Grace, 1936.)

These changes continue to the region of Aust, but from this point the level of the bed of the estuary rises, and although the height of high water (on spring tides) continues to rise as far as Gloucester, the level of low water instead of being lowered is raised rapidly until it coincides with the level of high water and the tidal wave has no influence above this point. It follows that the maximum range of tide is at Aust. The point at which the levels of high and low water coincide varies with the range of tide from Framilode (35 miles) on extreme neap tides to Upton-upon-Severn (66 miles) on extreme spring tides (Fig. 2*A*).

The foot of the tide wave (i.e. usually in an estuary the turn of tide) is increasingly retarded as it ascends the estuary, and the front of the wave (the crest being retarded only slightly) becomes increasingly steep until it may become in part vertical (Fig. 2*B*). The vertical front is the bore wave which dies out when the crest ceases to gain and is retarded a little relative to the foot. The steep front provides an increasingly short flood period the farther the wave travels. Spring tides flood for a shorter period than neap tides, so that from day to day there is less time lag during springs than during neaps, i.e. high-water springs are at about the same time on several successive days whereas neaps are very much later from day to day. The much increased range of spring tides and the slightly decreased time of flow causes a very considerable increase in the rate of the tidal currents during springs as compared with neaps.

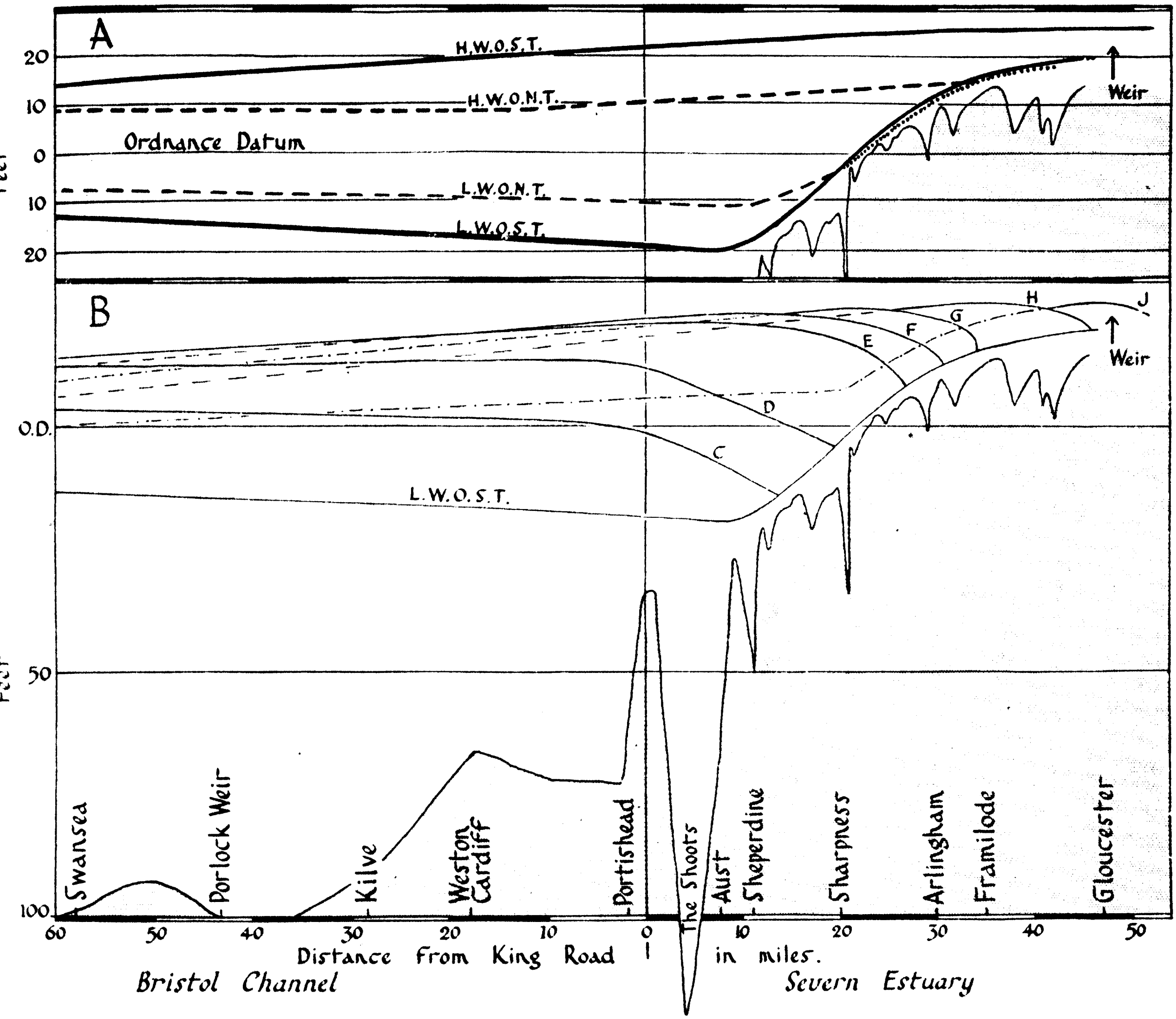


Fig. 2. A longitudinal section of the Bristol Channel and Severn Estuary showing: *A*, the level of high and low water of spring and neap tides; *B*, the change of form of the tide wave during spring tides as it passes up the estuary. (The foot of the wave is increasingly retarded until at Framilode part of the wave front is vertical, i.e. a bore wave. Subsequently the crest of the tide wave is retarded relative to the foot and the bore dies away); *C*, about half-tide at Swansea; *D*, 1 hr. before high water at Swansea (low water at Sharpness); *E*, high water at Swansea; *F*, high water at Avonmouth and Aust; *G*, high water at Sharpness (low water at about Framilode); *H*, high water at Framilode (low water at Gloucester); *J*, high water at Gloucester. The *approximate* relative times are: *C*, zero hour; *D*, 2 hr.; *E*, 3 hr.; *F*, 4 hr.; *G*, 4¾ hr.; *H*, 5½ hr.; *J*, 6½ hr.; i.e. 3½ hr. after high water at Swansea. (Drawn from data in Gibson, 1933.)

The large amount of water forced into the narrower reaches of the estuary during spring tides has not sufficient time during the ebb to drain away completely, and for this reason low water of spring tides is *higher* than low water of neap tides. Since the reverse is true of the open sea it follows that there is a point at which the level of low water does not change between springs and neaps. On the Severn this is at Sharpness (Fig. 2*A*).

Weirs at Gloucester (connected with canalization) bar the passage of all tides except those rising higher than 22 ft. above Ordnance Datum. Of these tides only a very few top the weir at Tewkesbury and reach Upton.

Tables 1–4 and the following paragraphs give the actual data illustrating these phenomena.

Table 1. *Tidal levels in the Severn Estuary* (*from Severn Barrage Committee's Report*, 1933)

Note. The abbreviations used to indicate tidal levels in this table are as follows: H.W.E. = high-water equinoctial tides; M.H.W.S. = mean high-water spring tides; M.H.W. = mean high water; M.H.W.N. = mean high-water neap tides; M.L.W. = mean low water; M.L.W.S. = mean low-water spring tides; L.W.E. = low-water equinoctial tides.

Description	Avonmouth ft.	New Passage (Severn Beach) ft.	Beachley (Aust) ft.	Sheperdine ft.	Severn Bridge (Sharpness) ft.	Framilode ft.	Gloucester ft.
H.W.E.	+26·0	—	—	—	—	—	—
M.H.W.S.	+22·5	+23·6	+23·4	+23·7	+25·5	+27·0	+26·0
M.H.W.	+17·8	+18·8	+18·5	+18·9	+19·9	+21·0	+21·8
M.H.W.N.	+11·9	+12·7	+12·3	+12·5	+13·4	—	—
Half-tide	+ 1·6	+ 2·4	+ 1·9	+ 3·4	+ 7·9	—	—
M.L.W.N.	− 9·9	− 9·7	−10·5	−10·0	− 5·2	+14·7	+18·8
M.L.W.	−14·6	−14·0	−14·8	−12·1	− 4·2	+15·3	+19·3
M.L.W.S.	−17·9	−17·1	−17·6	−12·6	− 3·4	+15·5	+19·5
L.W.E.	−21·4	—	—	—	—	—	—
Duration of rise:	h. m.	h. m.	h. m.	h. m.	h. m.		
Springs	5 14	4 54	4 47	3 57	2 53		
Means	5 42	5 23	5 20	4 36	3 28		
Neaps	6 29	6 15	6 16	5 53	4 27		
Duration of fall:							
Springs	7 03	7 22	7 30	8 20	9 23		
Means	6 42	7 01	7 04	7 48	8 56		
Neaps	6 17	6 31	6 30	6 55	8 19		
Duration of tides:							
Springs	12 17	12 16	12 17	12 17	12 16		
Means	12 24	12 24	12 24	12 24	12 24		
Neaps	12 46	12 46	12 46	12 48	12 48		
Range of tides:	ft.	ft.	ft.	ft.	ft.		
Equinoctials	47·4	47·7	—	—	—		
Springs	40·4	40·7	41·0	36·3	28·9		
Means	32·4	32·8	33·3	31·0	24·1		
Neaps	21·8	22·4	22·8	22·5	18·6		

High water on the days of Full and New Moon is at Avonmouth at 7.10, Severn Bridge at 7.58 and at Gloucester at 9.45 G.M.T.

The crest of the tidal wave on a spring tide rises 6 ft. between Penarth (Cardiff) and Gloucester, and on neaps the corresponding rise is of 3 ft. between Penarth and Sharpness —a neap tide does not pass Framilode. The main rise in the estuary bed occurs between Aust (Beachley) and Framilode (Fig. 2).

High water of spring tides is ½ hr. later on succeeding days. On neaps the corresponding figure is 1½ hr. (The mean is of course 50 min.—the difference between a solar and a lunar day.) The range of tide increases from Swansea to Beachley (Aust) and then declines owing to the rise in the level of low water. The lowest level reached during low water is not at Swansea but at Aust (Fig. 2*A*). The duration of the ebb increases as the estuary is ascended until it occupies all the time, i.e. there is no flood tide. Shortly after this point the river is tideless. The delay in the time of high water from Avonmouth to Gloucester is 152 min. on a spring tide, so that from Swansea to Gloucester it is about 215 min. It is obvious that one tidal wave has died away and the ebb has set in before another wave begins to pass up the Channel from Swansea. It follows that there is a period of nearly 3 hr. on springs, and more on neaps, when the whole body of estuary water is moving seawards.

Table 2. *More tidal levels in the Severn Estuary (from Gibson,* 1933)

Based on Ordnance datum. Accurate to ±0·25 ft.

	Mean spring tide				Mean neap tide			
Place	H.W.	L.W.	M.T.L.	Range ft.	H.W.	L.W.	M.T.L.	Range ft.
Cardiff (Penarth)	19·7	−16·7	+ 1·5	36·4	9·9	− 8·4	+ 0·7	18·3
Newport	21·1	−17·0	+ 2·0	38·1	—	—	—	—
Avonmouth	21·9	−18·4	+ 1·7	40·3	11·3	− 9·7	+ 0·8	21·0
Beachley (Aust)	22·2	−19·2	+ 1·5	41·4	11·4	−10·8	+ 0·3	22·2
Sharpness	24·5	− 3·3	+10·6	27·8	12·7	− 4·5	+ 4·1	17·2
Framilode	26·0	+16·0	+21·0	10·0	15·8	+15·8	+15·8	Zero
Gloucester	25·8	+20·0	+22·9	5·8	19·5	+19·5	+19·5	Zero

Table 3. *The time of high water at places in the Severn Estuary referred to the time of high water at Avonmouth (from Gibson,* 1933)

	Estuary	
Place	Spring	Neap
Avonmouth	0	0
Beachley (Aust)	+ 6 min.	+ 9 min.
Sharpness	+ 41 „	+51 „
Framilode	+ 86 „	No tide
Gloucester	+152 „	No tide

Table 4. *The duration of ebb and flow of tide at places in the Severn Estuary (from Gibson,* 1933)

	Times of ebb and flow				Ratio of times of ebb and flow	
	Spring		Neap			
	Ebb	Flow	Ebb	Flow		
Place	h. m.	h. m.	h. m.	h. m.	Spring	Neap
Penarth	6 32	5 52	6 12	6 32	1·11	0·95
Avonmouth	6 48	5 36	6 03	6 36	1·21	0·92
Beachley (Aust)	7 23	5 01	6 30	6 15	1·47	1·03
Sharpness	9 40	2 45	9 17	3 27	3·52	2·69
Framilode	11 20	1 00	—	—	—	—

A bore develops in a side channel opposite Sheperdine, but this loses itself in the sands about Guscar Rocks. The main bore usually appears about the Severn Bridge or near Brims Pill and travels up both the Noose and Frampton Channels at about 5 knots. (The foot of the tide wave travels from Aust to Sharpness at about 3½ knots.) The latter channel is tortuous and the bore arrives 7 min. later at Haywards Point than does the Noose Channel bore. How these two fuse is not described (Beechey, 1851), although it seems probable that the later bore merely dies away in the deeper water flooding back down the Frampton Channel. Indeed, the amount of water draining back down the Frampton Channel was so great on one occasion that the Noose Channel bore itself died away and only as the tide rose farther did a small bore redevelop about Newnham and proceed upstream (Cornish, quoted by Gibson, 1933). From Haywards Point the bore travels upstream to Framilode at a rate of nearly 7 knots. At Longney Point the wave stretches completely across the river and advances in an arc (lagging near the shore) at a rate of 10½ knots to Lower Parting, after which it gradually declines in velocity. The maximum speed ever observed was 14 knots at Rosemary and the maximum height in the centre 4½ ft. It is more usually about 3 ft. and near the shore some 4 or 5 ft. Boats in the middle of the river can ride the smooth wave, but near the shore the breaking wave would swamp or stove them in. The rate of travel of the bore wave from Haywards Point to Framilode remained unaltered between 1851 and 1926, but from Framilode to Lower Parting it has increased, taking now an observed minimum of 41 instead of 51 min. The highest bore wave develops on the highest spring tide. This normally occurs on the fifth tide (2½ days) after full and change of moon, and of course the best spring tides occur about the equinoxes. The higher the bore wave the faster it travels.

During floods from the upper river the rate of travel of the bore is increased because of the deeper water in the channel, but the bore wave is then not so high. During normal river flow after a period of floods the deeper, scoured channel causes a higher and faster bore than usual. Spring tides, on the other hand, appear to deposit silt in the reaches affected by the bore so that the bore wave towards the end of a period of springs is reduced in height and speed.

The ebb current usually turns as the bore wave passes, but occasionally during floods the water hangs for several minutes before beginning to run upstream. The flood current develops its maximum speed of about 4 knots within half an hour of the bore wave passing, and so has not half the speed of the bore wave.

Tidal currents about Avonmouth and Portishead are of the order of 2–5 knots ebb or flood according to the range of tide. In the narrow channel at the Shoots (English Stones) flood currents up to 5 knots and ebb currents up to 8 knots are recorded, and at the Aust narrows 6·0 knots on the flood and 6·5 knots on the ebb are normal maxima. At Sharpness, Beechey (1851) gives maxima of 4·4 knots on the flood and 5·3 knots on the ebb (of spring tides). At Slime Road (above Tites Point) 5·6 knots were recorded for the ebb and 2·8 for the flood. Following the bore wave in the Framilode to Lower Parting region flood currents of up to nearly 5 knots are recorded, and the ebb, depending so much on the state of the river, gives currents up to about 4 knots with a more normal flow of 1 or 2 knots.

The travel of a float with the tide may be very large. One float is recorded as travelling 35 miles from the Shoots to Framilode on a single spring-tide flood.

The silt content of estuary water

A notable result of the powerful tidal currents is the amount of silt kept in suspension in the middle reaches of the estuary.

Direct measurements of light penetration have not been made, but the suspended matter determinations described below will permit of comparisons with other rivers.

The determinations made during the present survey were carried out as follows: samples were obtained in pint bottles dipped below the surface by a man wading near the shore at low tide and from a boat in mid-channel at high tide. In the laboratory the bottles were shaken and arranged in a well-lighted room in a series according to opacity. Bottles from each end and the middle of the series were allowed to settle overnight and were then decanted. By a repetition of the process using smaller vessels the sediment was eventually transferred to a weighed specimen tube, washed twice in distilled water to remove salt, and evaporated to dryness at about 105° C. The tube and dry mud were then weighed and the original weight of the tube deducted. From the values so obtained a graph was constructed and intermediate readings made for the other samples. The method is crude but sufficient.

Readings are available for Porlock Weir, Blue Anchor, Weston, Aust and Arlingham Passage, from the present survey, for Framilode and the river Severn at Upton from an Admiralty survey (*Admiralty Report*, 1927), for Weston from Ebling (unpublished data) and for Portishead from Purchon (1937).

Table 5. *The amount of suspended matter in Bristol Channel water taken from the Old Pier at Weston-super-Mare at high water*

Month	No. of samples	Suspended matter in g./l.		
		Max.	Min.	Mean
1940: Feb.	Several	0·9	—	—
June	13	0·43	0·05	0·16
July	3	0·24	0·08	0·20*
Aug.	16	0·25	0·03	0·09
Sept.	11	0·25	0·06	0·13
Oct.	10	0·35	0·15	0·25
Nov.	3	0·61	0·51	0·54*
Dec.	1	—	—	0·59*
1941: Jan.	2	0·82	0·35	0·59*

* A 'mean' of one, two or three samples.

At Porlock large jars of water were obtained during spring tides in March 1940, at both high and low water. The value of 0·1 g./l. is therefore from a mixed sample and indicates that although silt is a clearly marked constituent of the water its amount is not considerable.

At Blue Anchor observations made during spring tides in April 1940 indicated that the muddy water which pours down channel at low water runs close by the rocky shore at the east end of the Bay. The large amount of suspended matter (1·4 g./l.) demonstrates this point. At the west end of the Bay the shingle slopes very gently into the water and the channel is offshore. The quiet inshore waters showed only a small amount of silt in suspension (0·06 g./l.). At high tide clean water comes in from seaward and silt ranging from 0·06 to 0·40 g./l. was present in four samples.

At Weston samples were taken and determined by Mr F. J. Ebling in February 1940, and from June 1940 to January 1941 samples were taken by Lieut. Wide for Dr L. H. Matthews and determined by the present author. The results are given in Table 5.

Although the winter samples are not numerous the table indicates that there is a gradual increase in the amount of sediment as summer gives way to winter. Ebling's maximum figure for February 1940 agrees closely with the January 1941 figures, and although more sediment may at times be present the figure probably indicates the normal maximum. A further analysis of the summer values is given in Table 6. Blue water is occasionally seen at Weston.

At low water at Portishead, Purchon (1937) got much higher figures—his maximum was 5·70 g./l. and the mean of ten readings between September 1936 and April 1937 was 1·92 g./l.

For a whole month during March and April, and again in August and September 1940, samples were taken daily by Captain W. Groves of the Aust-Beachley Ferry and by Mr W. Hayward of the Newnham-Arlingham Ferry at both high and low water. The analyses of these samples gave figures which are summarized in Table 6.

Table 6. *The amount of suspended matter in samples of Severn Estuary water taken at Aust and Arlingham Passage showing the difference between spring and neap tides*

A spring tide has been taken as any tide rising to more than 26 ft., and a neap tide one rising to less than 20 ft. at Sharpness as predicted in Arrowsmith's Bristol Channel Tide Tables for 1940.

			Suspended matter in g./l.							
			Winter (March)				Summer (August)			
Place	Period	State of tide	No. of samples	Max.	Min.	Mean	No. of samples	Max.	Min.	Mean
Weston	Spring tides	H.W.	—	—	—	—	14	0·25	0·05	0·14
		L.W.	—	—	—	—	9	0·14	0·03	0·09
	Neap tides	H.W.	—	—	—	—	8	0·13	0·04	0·07
		L.W.	—	—	—	—	7	0·46	0·05	0·14
Aust	Spring tides	H.W.	12	2·62	0·11	0·96	11	1·04	0·12	0·48
		L.W.	12	2·95	0·35	1·13	10	2·42	0·15	0·62
	Neap tides	H.W.	10	1·23	0·08	0·49	10	0·49	0·04	0·18
		L.W.	10	3·33	0·23	0·98	9	2·25	0·10	0·56
Arlingham Passage	Spring tides	H.W.	12	4·15	0·63	2·48	14	4·15	0·09	1·29
		L.W.	12	0·45	0·08	0·18	14	1·80	0·10	0·42
	Neap tides	H.W.	8	0·50	0·04	0·25	8	0·33	0·04	0·15
		L.W.	9	0·16	0·07	0·09	8	0·12	0·04	0·08

With data of this kind when variations from one day to the next may amount, exceptionally, to as much as 3400%, individual observations are well nigh useless and only means can have any significance. From Table 6 it can be seen that there is more sediment in the water in winter than in summer, and that at Arlingham the maximum sediment is present at high water while the reverse is true of Aust. At Arlingham Passage neap tides do not affect the river, but spring tides do so very markedly. The effect is greater in summer than in winter, and there is some indication in the summer value 0·42 g./l. for low water of spring tides that all the turbulent water has not drained away by low tide. At Aust the stronger currents during spring tides cause more sediment to be carried in the water both in summer and winter. They also increase the high-water sediment more than they do the low-water sediment, so that on springs the sediment is approximately the same at both high and low water. The maximum values recorded agree fairly well with the maximum value of 5·7 g./l. for Portishead (Purchon, 1937).

It is possible to add to the above information mainly from Admiralty sources.

Gibson (1933) quotes Ham, who found a mean concentration (in 1837) of 0·58 g./l. of suspended matter in five samples between Avonmouth and the Usk mouth. Gibson gives figures for 1926 at Portishead, and in six samples taken near the bottom the suspended matter ranged from 0·50 to 0·65 with a mean of 0·58 g./l. Despite this agreement the figures are low when compared with Purchon's maximum of 5·7 for Portishead and other figures for the Avonmouth region quoted above and below.

Tables 7 and 8 are quoted from Gibson (1933) and have had the units changed from volume to weight, using factors given in the *Admiralty Report* (1927). Tables 9 and 10 have been extracted from the detailed tables given in this same *Admiralty Report*.

Table 7. *The mean silt content of Severn Estuary water at Avonmouth at varying depths during spring and neap tides from readings taken at high water, half ebb, low water and half flood (from Gibson,* 1933)

Depth as fraction of whole depth	Suspended matter in g./l.	
	Spring tides	Neap tides
¼	2·18	0·61
½	2·68	1·18
¾	2·93	1·86

Table 8. *The mean silt content of Severn Estuary water at various places from readings taken at all depths and during both spring, neap and ordinary tides (from Gibson,* 1933)

Place	Suspended matter in g./l.			
	H.W.	½ ebb	L.W.	½ flood
Avonmouth	1·20	1·64	2·68	2·86
The Shoots (Severn Beach)	1·67	2·06	2·82	3·60
Aust	2·27	2·31	5·55	3·30
Framilode: Spring tides	4·00	0·82	0·43	1·41
Neap tides*	0·10	0·06	0·13	0·07

* Neap tides do not reach Framilode.

Table 9. *The maximum and minimum observed values of suspended matter in Severn Estuary water in samples taken at various places, at high and low water from a depth equal to one-quarter of the total channel depth at the time of sampling (extracted from Admiralty Report,* 1927)

Place	Suspended matter in g./l.			
	High water		Low water	
	Max.	Min.	Max.	Min.
Avonmouth	4·42	0·22	3·71	0·67
Shoots	1·73	0·12	4·31	0·60
Aust	3·20*	0·70*	6·02*	0·97*
Framilode	5·25*	0·02	0·68	0·04

* High value compared with data from the present survey.

Table 10. *Observed values of suspended matter in samples of Severn Estuary water taken at Aust at high and low water of spring and neap tides at a depth of one-quarter of the full depth available (taken from Admiralty Report,* 1927)

Place	Period	State of tide	Suspended matter in g./l.	
			Winter	Summer
Aust	Spring tides	H.W.	3·20*	2·70*
		L.W.	3·50*	2·17
	Neap tides	H.W.	1·69*	—
			0·70	—
		L.W.	1·24	—
			0·97	—

* High value compared with data from the present survey.

As a mean for all states of tide at all seasons and all depths Gibson (1933) gives an approximate figure of 2 g./l. for the water between Avonmouth and the Shoots. From Tables 7 and 8 he says (paragraph 38): 'The proportion of silt in suspension in the estuary is greatest about low water and half flood and is at a minimum at high water (see Table 8). It is somewhat greater in dry weather than in wet weather and increases from the surface downwards. These points are brought out by the following figures (Table 7 here) which give the means of the observations at Avonmouth. From these it appears that the greater turbulence of the water due to the increased velocity of the spring tidal currents brings into suspension much more of the deposited silt, and that this effect is much more pronounced over the upper half of the depth than the lower half.'

These deductions agree with those made above, but from a consideration of Table 6 it is obvious that the first statement made by Gibson applies only to the part of the estuary about Avonmouth and Aust. The reverse is true of higher reaches. This is because in the narrower reaches of the estuary—from about Aust to Arlingham—the tidal currents stir up the silt lying on the bottom and on the banks and carry it in suspension. There is, therefore, a zone of very muddy water which washes to and fro with the tide, and the observations indicate that the muddier parts of the zone ebb down to Aust and below at low water but are washed above Aust at high water. This accounts for the higher silt concentration at low water. Similarly, the zone is carried up to Arlingham on the flood but is washed clear by river water on the ebb producing the highest silt concentrations at high tide.

During spring tides more silt is stirred up by the increased currents giving higher suspended matter concentrations in all reaches, and, as Gibson has shown, bringing more silt to the surface waters than on lesser tides. The bottom waters already carry so much that they are but little affected. It follows that much of this suspended matter settles out as the tidal range decreases and rests on the bed during neap tides.

It has been assumed that the zone of turbid water is a function of the shape and current system of the estuary and that it occupies the same reaches in summer and winter alike. During fresh-water floods the estuarine brackish water zone is pushed seawards, so that any given reach of the estuary is filled, at a corresponding state of tide, by more saline water in summer than in winter (Fig. 7). It follows that the maximum silt content will occur in samples of water of higher salinity in summer than in winter. All available samples have been grouped on a salinity basis and the mean silt content of each group plotted in Fig. 3. This shows that although there is less silt in summer than in winter (0·54 against 0·79 g./l. for all samples of less salinity than 25 g./l.) the summer maximum does occur in more saline waters, thus supporting the assumption made above.

The figures quoted in Table 8 for Aust are means of samples at all depths. It might be expected that these means would be higher than the surface values (Table 6), since the silt content increases with depth (Table 7). The original data (*Admiralty Report*, 1927) have been consulted and surface values extracted (Tables 9 and 10). Even these values range higher than the 1940 samples at Aust, and although it is possible that this excess is due to the Admiralty samples being taken at ¼ depth instead of at the surface itself, it is also possible that the water was definitely more turbid in 1926 and 1927 than in 1940, i.e. the difference may be evidence of year to year variations.

Returning to Gibson's report we find values given for the silt content of river water. At Upton, the Severn contained 0·06 g./l. both during normal flow and when in spate.

At Framilode during neaps (i.e. a non-tidal period) a value of 0·1 g./l. was recorded. The Wye at Biggesweir had 0·06 g./l. during normal flow and 0·04 when in flood. In Paragraph 40 Gibson says: 'A comparison of the concentration in the tidal portion of the river between Avonmouth and Beachley (mean value 2·6 g./l.) with that for the Severn or Wye at the limit of tidal action (0·06 g./l.), shows that the silt content is 40 times as great in the estuary proper as in the river. These results indicate very clearly that the great turbidity of the estuarine water is due to the stirring up during the latter portion of the ebb tide and the first part of the flood, of the silt lying on the bed of the estuary, which represents the gradual accumulation of material brought down by the rivers during many years. It also shows that the extreme turbidity of the lower part of the Avon and Wye is due to silt brought in from the estuary on the flood tide rather than silt brought down by the rivers themselves.'

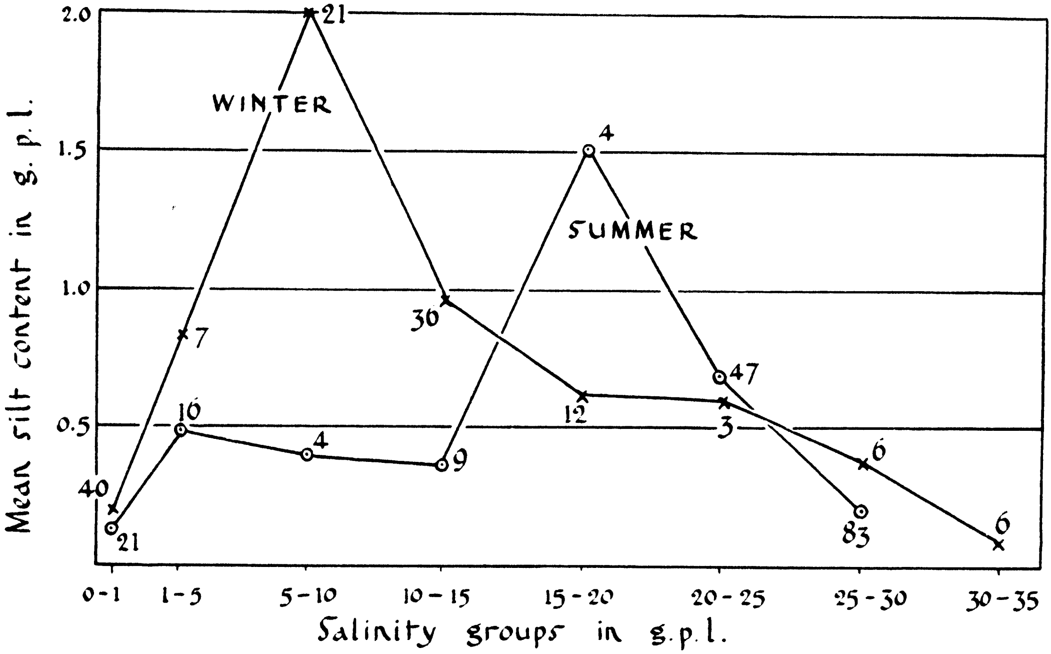


Fig. 3. The turbidity of Severn Estuary water. A graph showing the mean silt content of samples in different salinity ranges and the difference between winter and summer. The numbers represent the number of samples from which the mean for each point was obtained.

Gibson also points out that if the Severn and Wye were bringing down as much as 0·12 g./l. this would represent 650,000 tons per annum or, distributed over the 35 sq. miles of estuary above Severn Beach (the Shoots), a layer 0·24 in. deep. If the Parrett, Avon and Usk are included the figure is 880,000 tons of material and, spread over the 332 sq. miles of the estuary down to Barry, this represents a layer 0·035 in. thick—4 in. in 100 years.

Another interesting calculation can be made. Gibson (1933) gives certain approximate figures as follows: mean silt content of water between Avonmouth and Severn Beach under all conditions = 2 g./l.; mean flow of Severn and Wye = 6270 cusecs; mean rate of flow of a spring ebb past Severn Beach = 200 × flow of Severn and Wye; approximate duration of a spring ebb = 7 hr. Therefore, the amount of silt passing Severn Beach on an ebb tide is approximately 1,800,000 tons, and from the above-quoted (deliberate) over-estimates of the silt brought down by the rivers it appears that the Severn and Wye could contribute the silt washed about on spring tides in as little as 2·7 years and all the rivers in 2·0 years. These figures, based on a variety of approximations, are interesting in being so small. They make it all the more reasonable to accept Gibson's assumption that all the silt in the estuary is an accumulation of material from the rivers. None-the-less, it was believed by Sollas (1883), from a microscopical examination of Severn deposits, that the Severn mud came from the sea. Similarly, it was recently shown that a fairly rapid decrease in the capacity of the Mersey Estuary above Liverpool (68,000,000 tons in 20 years or 5% of the total capacity) could only have been produced by an influx of sediment from the sea (Southgate *et al.* 1938). There is reason to believe that this last process is reversible, and it might thus appear that some estuaries have phases of bank accretion in excess of erosion, followed by erosion in excess of accretion, and that during the former process the material in suspension and newly deposited may be of marine origin. In the long run it seems probable that permanent accretions are due to silt brought down from the river although it is possible to imagine periods when the banks are built up of marine material and in subsequent years the river material goes out to sea to replace it.

Salinity data

Apart from isolated samples taken at all collecting stations at the time of low water the salinity determinations made during the present survey can be divided into two groups, a series taken by Lieut. Wide for Dr L. H. Matthews at Weston and a series taken every day for one month during March 1940 (the winter series) and during August 1940 (the summer series) at both high and low water at Aust and at Arlingham Passage. These correspond with the series for the determinations of suspended matter. March and April are late for a 'winter' series of samples. This was due to the peculiar weather conditions of the 1939–40 winter. The salinities determined by Rees (1939) for Cardiff Roads indicated a minimum in February, and it was decided to take samples during that month. Unfortunately, the great frosts held up the river flow and conditions were abnormal. Two weeks after the thaw were allowed for the excessive flood water to run off, and sampling was then begun on 5 March 1940. In addition, values for Cardiff Roads over a whole year (Rees, 1939) and a series taken by the Admiralty in 1926 (*Admiralty Report*, 1927) are available.

Figs. 4–8 have been prepared from the new data. The actual salinities have not been graphed, but smoothed values—obtained by adding three successive readings and plotting the mean—have been used. At Aust the summer salinities are seen to be little affected either by the state or range of tide (Fig. 4). That is to say, whether the sample was taken at high or low water, during springs or neaps the maximum variation observed was only 4 g./l. An exception was recorded on 10 September when at low water the salinity was only 12·2 g./l., although the high-water salinity on that day and the salinities on the previous and succeeding days were unaffected. This exceptional value may have been due to a flood from the upper river* or some local sampling incident.

In winter day-to-day fluctuations are marked, and the range of tide has an influence particularly on the low-water salinity. On one or two occasions the water was actually fresh at low water of neap tides. A feature of both high- and low-water salinities is the time lag of the maximum salinity behind the highest tides. During early March this lag amounted to 4 days.

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* No flood appears in the Bewdley gauge readings.

At Arlingham Passage—which lies close to the upper limit of the effect of neap tides—the effect of the range of tide is clear (Fig. 5). Floods from the upper river have a large effect, and wide fluctuations may take place in the salinity of the water at high tide from day to day, but the smoothed curves give a general picture of the tidal effect. In winter the low-water salinity is scarcely affected even by the highest tides of the year, and it remains near zero. The high-water salinity is affected during springs only and attained a maximum of 10·2 g./l. on 27 March. In summer the water remains fresh during the lowest neaps, but the salinity at high and low water may attain, during springs, the high values of 24·1 and 13·2 g./l. respectively. The low-water salinity in summer may exceed the high-water salinity in winter. The high salt content of the water at low spring tide is due to the fact that so much water is forced up the narrow part of the river by the high tides that it has insufficient time to flow away during the ebb and some is retained in the upper reaches until the tides slack off towards neaps. Correlated with this high salinity is the fact that the level of low water in these upper reaches is higher during springs than during neaps (Fig. 2*A*).

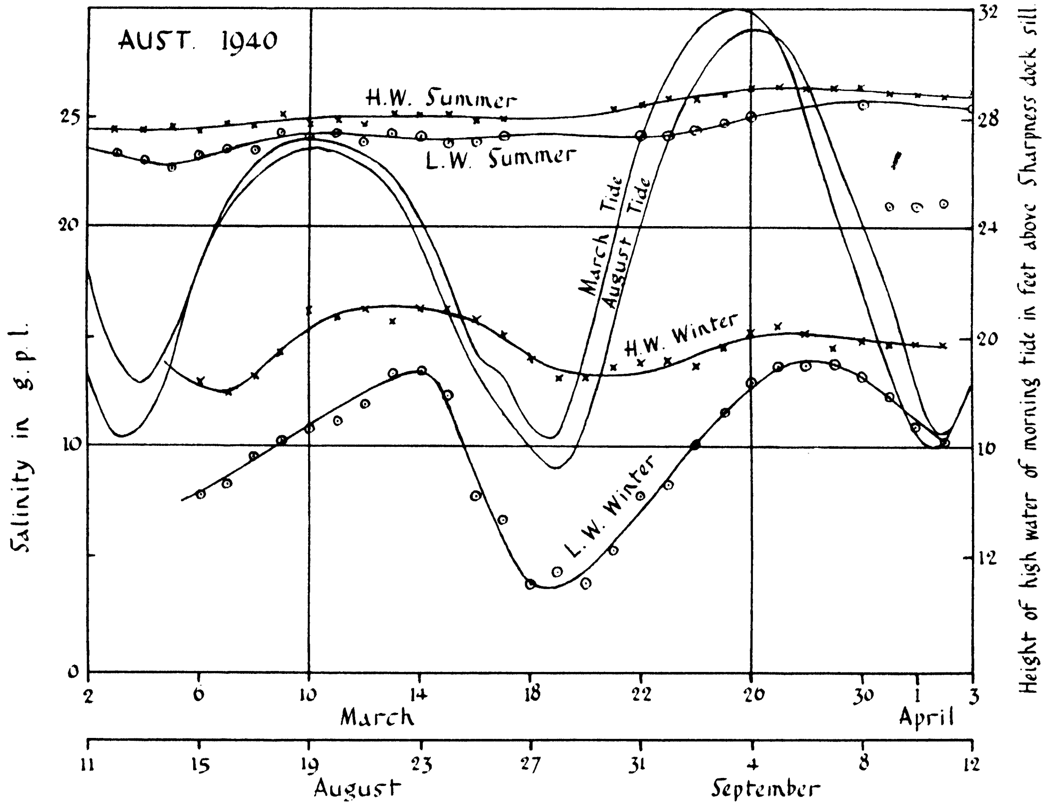

Fig. 4. The salinity of water samples from Aust taken at high and low water in winter and summer, 1940 (smoothed curves).

Data from Mr F. J. Ebling and Dr L. H. Matthews for 1940 make it possible to present a curve showing the seasonal change of salinity at Weston (Fig. 6). There is an annual change of much greater range than the tidal fluctuations. These latter have only once been greater than 1 g./l. and are usually much less. The seasonal change was from a maximum in October of 28·5 to a minimum in February of 21·8 g./l. The increase in salinity during spring and summer was more gradual than the very sudden lowering in November and December.

From Figs. 4–6 it is possible to define the salinity conditions which obtained during 1940 at Weston, Aust and Arlingham. Occasional determinations are available from elsewhere. From these data Fig. 7 has been constructed. The effect of the winter freshwater flow is very marked. In the region below Aust the seasonal variation is much greater than the tidal variation (i.e. the difference between high and low water salinity), indeed the tidal variation in salinity is often inconsiderable, particularly under the more stable conditions of summer. At Weston the low-water salinity was sometimes a little greater than the high-water value, and the means of numerous determinations during August and September 1940 show that the high-water value exceeded the low-water value by 0·1 and 0·2 g./l. respectively. In February 1940 this difference was only 1·0 g./l. and so corresponds with previous records by Rees (1939) for Cardiff Roads.

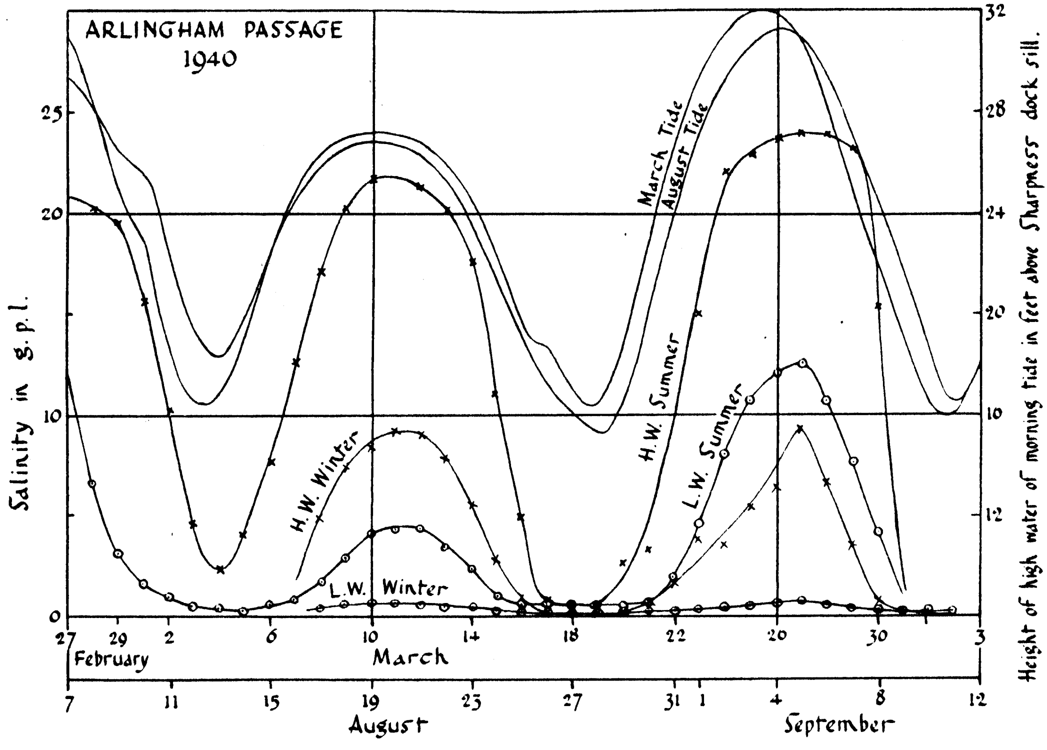

Fig. 5. The salinity of water samples from Arlingham Passage taken at high and low water in winter and summer, 1940 (smoothed curves).

Above Aust and extending above Arlingham Passage is the zone of maximum variation, the winter zone of maximum variation lying mainly between Aust and Sharpness and the summer zone from about Sharpness to Arlingham (Fig. 8).

The full extent of the penetration of salt water is not known, since only low-water samples are available from above Arlingham. The single summer reading of 0·7 g./l. from

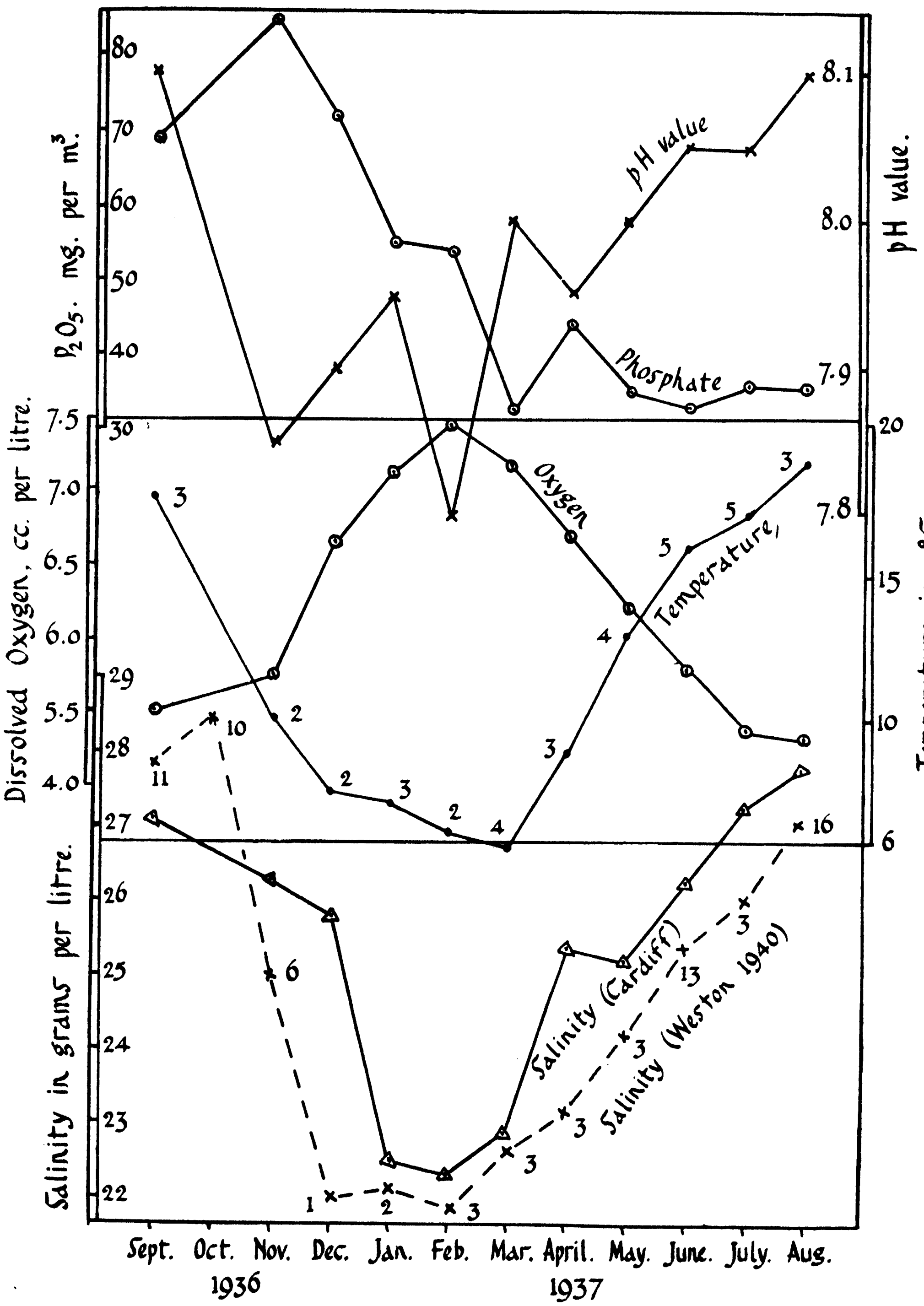

Fig. 6. Analyses of water samples taken at high water from Cardiff Roads in 1936–7 from Rees (1939) and salinity figures for Weston in 1940. The numbers in brackets refer to the number of samples averaged for each point (all Rees's analyses are the means of the samples shown on the temperature curve).

Ashleworth Ferry is probably not significant (see below). It is known, however, that salt water reaches Epney on spring tides and not on neap tides.

Some variations in salinity that have been recorded among isolated samples are also shown in Fig. 7. The variations between Weston and Porlock are small. At Portishead samples taken by Purchon in 1936 (unpublished) show small differences in summer (line *B*), but in winter they show very large variations. No reading is below the values for the winter of 1940, but some exceedingly high salinities were recorded in March 1937 (line *A*).

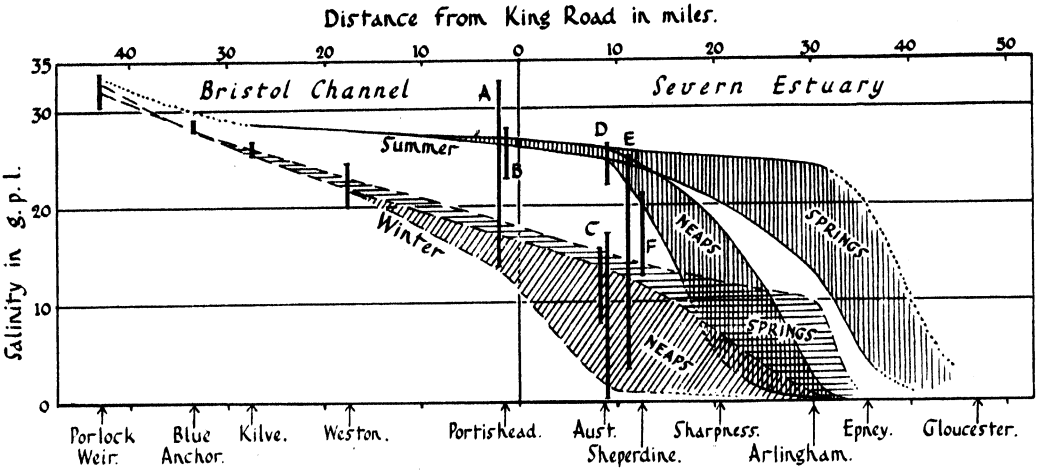

Fig. 7. The salinity of Bristol Channel and Severn Estuary water in 1940 showing tidal and seasonal changes. The vertical black lines indicate the range of additional observations: *A*, during winter, 1937, and *B*, during summer, 1936 (Purchon, 1937); *C* and *D*, at Aust at different periods; *E*, at Oldbury during all seasons in 1937–8 (unpublished data from A. J. Lloyd); *F*, at Sheperdine at different periods. The winter records by Purchon (line *A*) are exceptionally high.

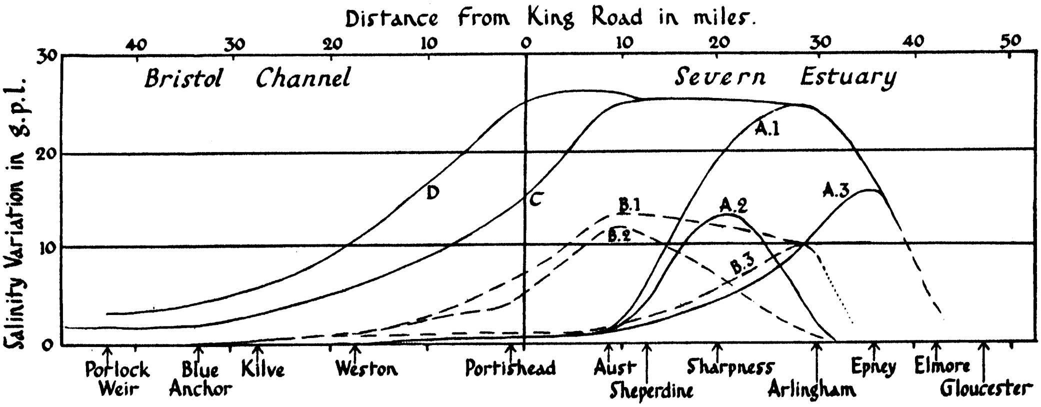

Fig. 8. The maximum salinity variations observed in the Bristol Channel and Severn Estuary. *A*, summer, 1940 (*A*1, during a whole month; *A*2, during neap tides; *A*3, during spring tides); *B*, winter, 1940 (*B*1, during a whole month; *B*2, during neap tides; *B*3, during spring tides); *C*, during the whole of 1939–40; *D*, including all records.

Recorded variations at Aust (lines *C* and *D*) and Arlingham are not exceptional, and at Oldbury (line *E*) figures from A. J. Lloyd for 1938 fit within the limits of the graph. At Sheperdine, however, the values determined from a few samples taken at low water in spring 1939 do not fit the 1940 graph at all, being much higher (line *F*).

It is obvious that large variations occur from year to year in the region of Portishead, Aust and Sheperdine, and that the curves given are applicable to the year 1940 only.

Salinity data are available for the Cardiff Roads (Rees, 1939) and for the region Avonmouth to Aust (Gibson, 1933; *Admiralty Report*, 1927). From Rees's data it is possible to construct a curve for the mean high-water salinity at Cardiff Roads throughout the year. Compared with the corresponding curve for Weston, just across the river, the Roads figures for 1936–7 are 1 g./l. higher than the 1940 figures for Weston (Fig. 6). This is in agreement with the isolated records mentioned above which also tended to be higher than the 1940 figures.

Gibson (1933) summarizes Admiralty salinity data in the following words:

> In the inner part of the Bristol Channel the salinity is about 34. Between Beachley (Aust) and Avonmouth the average value for all states of tide and of weather is about 17, and the water in that region is therefore approximately one-half sea water and one-half fresh.
>
> The following are the mean values of the salinity for all tides and conditions of weather throughout the depth of the river:
>
> Table 11
>
> | | At H.W. | At L.W. |
> |---|---|---|
> | Avonmouth | 22·52 | 15·78 |
> | The Shoots (Severn Beach English Stones) | 22·57 | 13·97 |
> | Beachley (Aust) | 16·99 | 11·26 |
> | Framilode*: Springs | 6·91 | 0·13 |
> | Neaps | 0·10 | 0·09 |
>
> * Samples at half-depth only.
>
> During wet weather the salinity is less than in dry weather. Between Aust and Avonmouth the wet weather figure is about 65% of the dry weather figure while at Framilode the corresponding relationship is 42%.
>
> The observations show that at all stages of the tide the salinity is the same at all depths, indicating that the admixture of sea and river water is thorough at these points.
>
> It is often stated that when the flood tide sets into an estuary the sea water advances in a dense layer underlying the lighter fresh water, and that on the ebb tide the advancing river water overlies the denser sea water. The salinity observations show, however, that this is definitely not the case in the Severn.
>
> This is probably due to the great turbulence occasioned by the rapid changes of section and the high velocities at Aust and the English Stones, which cause a very effective mixing of the water.

A comparison with Gibson's figures can be made by calculating means for the 1940 figures, and these are presented in Table 12 for Weston, Aust and Arlingham.

These means are not of considerable value as definitions of biological salinity conditions, but they do yield a picture of the decreasing salinity from Weston to Arlingham. The figures in brackets are from Table 11 and from *Admiralty Report* (1927) and show that, by comparison, the 1926–7 figures are low. Since it has been suggested above that the 1940 figures themselves were low, it follows either that the 1926–7 samples were inadequate to give a true mean value or that 1926–7 was a wet season. An examination of the original figures (*Admiralty Report*, 1927) shows that seventy-two salinity samples were taken at Aust. These represent samples taken at three depths, making twenty-four series, and since some of these series were on the same day and others at half-flood or half-ebb the values in Table 11 are based on samples taken on only 12 different days.

It seems probable, therefore, although these 12 days were carefully spaced over springs, ordinary tides and neaps, that the means for 1940 are nearer the normal values.

The real value of these Admiralty figures in connexion with the present survey is that they prove the absence of a vertical salinity gradient at any state of tide. This permits the acceptance of the surface salinities taken during the present survey as true indicators of the salinity at any given station. Although no figures are quoted by Gibson it is possible to extract the data from the *Admiralty Report* (1927), and in view of the importance of this point the figures are given here (Table 13).

Table 12. *The mean salinities of Bristol Channel and Severn Estuary water in* 1940 *for comparison with samples taken by the Admiralty in* 1926–7 (*in brackets*)

	Weston	Aust	Arlingham
	Parts per thousand		
Mean salinities at high water in summer	27·3	25·4 (18·6)	13·7
,, ,, winter	22·1	14·6 (15·3)	3·7
,, ,, winter and summer	24·7	20·0 (17·0)	8·7 (6·9)
Mean salinities at low water in summer	27·4	24·0 (14·1)	3·6
,, ,, winter	21·7	9·9 (8·4)	0·3
,, ,, winter and summer	24·6	17·0 (11·3)	1·9 (0·13)
Mean salinities in winter at high and low water	21·9	12·3	2·0
,, summer ,,	27·4	24·7	8·7
General mean salinity for high water and low water in winter and summer	24·7	18·5	5·3
	Percentages		
The general mean salinities expressed as percentage sea water	73	54	16
The mean winter salinity (wet weather) expressed as a percentage of the mean summer salinity (dry weather) indicating the effect of floods:			
At high water	81	58	27
At low water	79	41	7
At both high and low water	80	50 (65)	23 (42)

Table 13. *The mean salinities in grams per litre of water samples taken at different depths in the Severn Estuary showing the absence of a vertical salinity gradient* (*extracted from data in Admiralty Report*, 1927)

	Avonmouth		The Shoots		Beachley (Aust)	
	¼ depth	¾ depth	¼ depth	¾ depth	¼ depth	¾ depth
At high water of all tides	22·5	22·6	22·8	22·5	16·7	17·3
At half-ebb of all tides	20·4	20·7	16·9	17·3	11·1	11·6
At low water of all tides	15·9	15·8	17·8	18·3	11·3	11·2
At half-flood of all tides	19·1	19·3	17·5	17·5	15·0	15·5
During spring tides (all states of ebb and flow)	20·0	20·2	17·3	17·5	14·0	14·3
During ordinary tides (all states of ebb and flow)	21·1	21·3	18·8	19·3	13·0	13·9
During neap tides (all states of ebb and flow)	17·2	17·4	17·1	16·9	13·7	13·5
During wet weather (all tides and states of tide)	16·2	16·5	12·6	12·9	10·8	11·3
During dry weather (all tides and states of tide)	22·7	22·8	22·9	23·0	16·1	16·4
General mean for each station	19·4	19·6	17·7	17·9	13·5	13·9
Mean for whole of samples at all three stations (72 at each depth)	—	—	16·9	17·1	—	—

The largest observed difference on any occasion was at Aust at half-flood on an ordinary tide during wet weather and amounted to 3·1 g./l. This was very exceptional, and of the seventy-two pairs of observations (surface and bottom) there were actually nineteen which showed a slightly greater salinity at the surface—not at the bottom, and the largest difference in this direction was 1·7 g./l.

The nature of the fresh water entering the estuary from the Severn is of importance to the fauna in the uppermost reaches, and so far no evidence of its nature has been presented beyond the value of 0·7 g./l. obtained on analysis by the usual sea-water chloride titration of a sample from Ashleworth Ferry. The probable origin of this relatively large amount of salts in solution is not far to seek. There is a saline water spa at Droitwich, and analyses of the River Salwarpe water (near Droitwich) and of River Avon water from Tewkesbury have been given by Cooper (Sexton, 1939). These two tributaries of the Severn contain total solids (dried at 180° C.) from 0·8 to 3·2 g./l. The actual salts present make the water much more like diluted sea water than is normal for inland rivers.

Other physical data

Rees (1939) has given figures of analyses made on samples of estuary water from Cardiff Roads during the period September 1936 to August 1937. He showed that several factors were correlated with salinity (Fig. 6). The salinity fell to a minimum in February and was highest in August. Temperature varied directly with the salinity and dissolved oxygen varied inversely. The hydrogen-ion concentration varied directly but rather irregularly, while phosphates did not show correlation. The variations shown are not abnormal and are not likely to affect the fauna adversely. The correlation with salinity probably means that the sea water is pushed seawards in winter by increased river flow and gives way to fresher estuarine water which is somewhat deoxygenated by the stirring up of silt. The salinity data agrees quite closely with the Weston data (see above). Oxygen values from F. J. Ebling (unpublished) for Weston in 1940 and from Purchon (1937) for Portishead vary from 70 to 100% saturation and agree with Rees's figures in showing no signs of unfavourable conditions. *p*H values varied from 7·9 to 8·1 as at Cardiff Roads. For Portishead, Purchon's temperature records vary from 4·8° C. in March to 19·4° C. in September, thus agreeing closely with Rees's figures. For Weston, however, Ebling's temperature records go down to 2·0° C. in February 1940, although it was normal at 5° C. in March. The low figures for February are indicative of the exceptional weather of that winter.

BIOLOGICAL DATA

All available data concerning the distribution of animals in the estuary have been presented in the form of a fauna list (Bassindale, 1940).

The flora

The shores of the Bristol Channel are clothed with large brown algae wherever rocks provide a suitable holdfast. In the region of Lynmouth and Porlock Weir these large algae are mutilated by the rubbing of shingle and stones moved by wave action. Towards Kilve and at Weston and Portishead the growths are good wherever rocks occur, but the conditions are muddy. In the estuary at Aust and Sheperdine good growths again occur and some very large plants, notably of *Ascophyllum nodosum*, may be found. *Fucus vesiculosus* and *Enteromorpha* only have been recorded above Sharpness (*Fucus* at Tites Point, Purton and *Enteromorpha* at Epney). *Chondrus crispus* is widely distributed up to Sheperdine. More details of plant distribution have been given elsewhere with the accounts of each collecting station (Bassindale, 1942*a*).

The general fauna

The faunistic records can be divided into two parts. Those actually made during the present survey (this includes records made by Purchon at Portishead (1937), by Matthews from the Somerset coast (1923) and by Ebling at Weston (unpublished)) and those made by much earlier workers. Considering only marine animals and omitting deep-water species and planktonic forms or those capable of rapid movement, we can obtain a general picture of the stable fauna of the estuarine shores.

The data for all available records are summarized in Fig. 9. The hollow columns erected on the base-line indicate the number of species recorded from different stations. To provide a better comparison in the Bristol Channel where collections by many different workers have been made the records have been grouped in 10 mile zones (0–10, 10–20, etc.), and the number of species present in the zone plotted in solid columns on the half-way line (5, 15, 25, etc.). These zones each contain one of the collecting stations of the present survey, and the recent records constitute the main recorded fauna of any zone. The 'zoned' records of the channel are, therefore, comparable with the estuarine records from above Avonmouth, where records other than present-day ones are extremely rare.

At Ilfracombe all records are by earlier workers and much intensive work was done there. In Fig. 9 the solid column includes all definite records for Ilfracombe or Combe Martin Bay. The next part of the column shows the number of ostracods recorded by Norman & Scott (1906). No other ostracods are recorded except for a single species at Weston, and it is certain that this apparent scarcity is due to the absence of work on the group. In addition to definite records for Ilfracombe there are many species recorded from the 'Devon coast', 'North Devon coast' or even 'south-west England' which most probably occur at Ilfracombe and possibly farther along the Channel towards Avonmouth. When these records are included (and the list cannot be complete) a grand total, for the fauna of Ilfracombe, of 279 species is obtained.

From the graph it can be seen that there is a large fauna of over seventy macroscopic species at stations in the Channel from Minehead to Avonmouth, and that thereafter the fauna falls away rapidly. The single species which penetrates to Ashleworth Ferry is really a brackish water form—*Gammarus zaddachi*.

If it is assumed that any marine animal is present at all stations seaward of the highest station at which it was recorded, then a fauna curve is obtained which rises much more steeply towards Ilfracombe than do the columns of actual records. This is partly due to the fact that the larger the fauna present, the more intensive must be the collecting to obtain a proportionate collection. The curve so obtained (Fig. 9) lies close to the column heads in the estuary and in zone 1 (0–10 miles) of the Channel, but from there it rises steeply to an assumed fauna at Ilfracombe of 404 species. This very high figure means that there are many species which have been recorded from the upper end of the Bristol Channel but not from Ilfracombe. Accordingly, the records have been examined to discover the identity of these 115 species. Only ten belonged to groups known to have been carefully collected from Ilfracombe (Porifera, Coelenterata and Polyzoa), while seventy-six belonged to the polychaetes and molluscs, of which groups very few species are recorded from Ilfracombe. Of the remaining species some are mud living (*Phascolosoma vulgare*), others are brackish water forms (*Gammarus zaddachi*), and there are some species whose

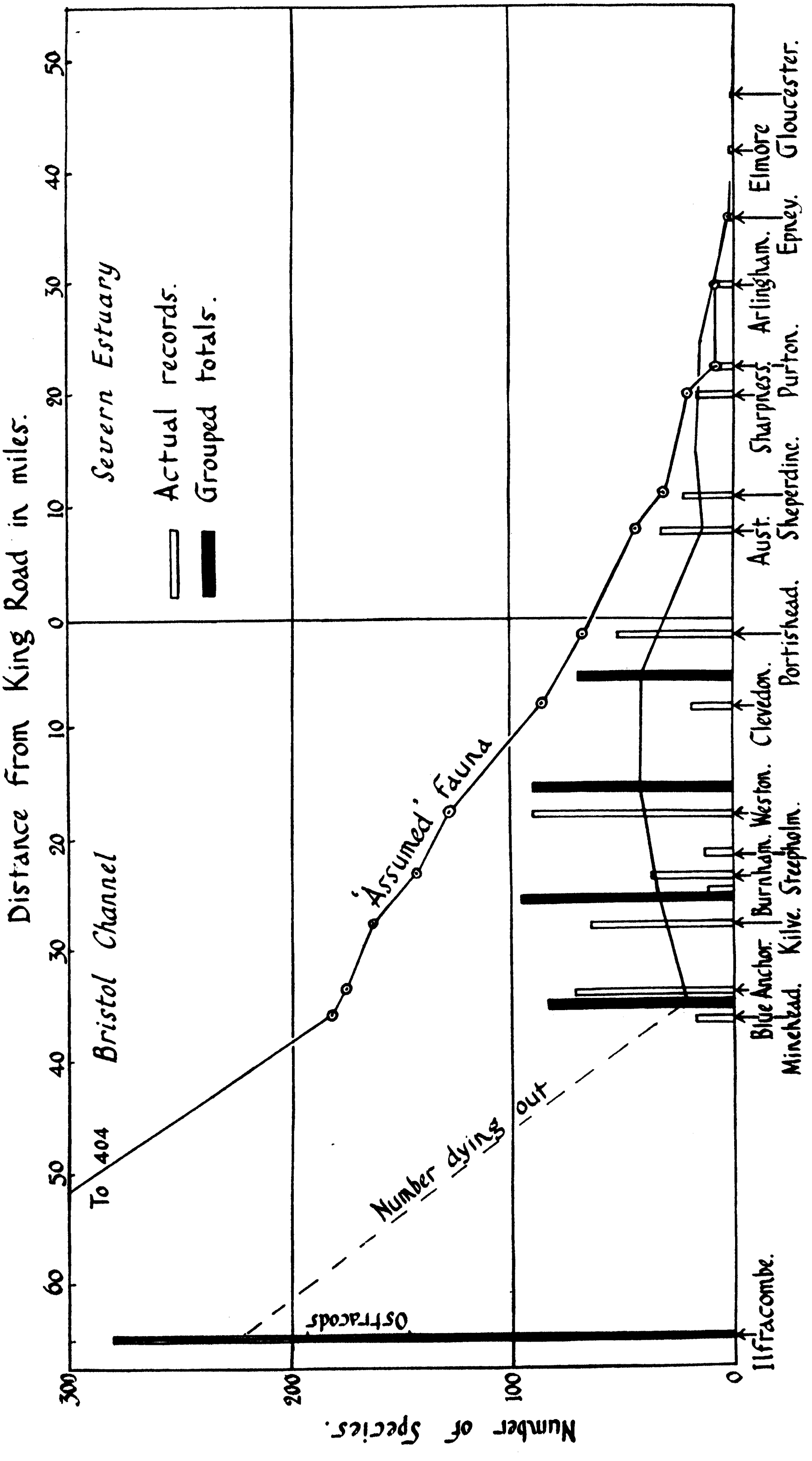

Fig. 9. The numbers of species of marine intertidal animals recorded from all sources (excluding pelagic forms).

apparent absence from Ilfracombe is obviously due to the absence of definite records (*Cancer pagurus* and *Balanus perforatus*). It seems probable that until the intensity of collecting is more balanced a comparison of the Ilfracombe fauna with that of the upper Bristol Channel is of little value except in certain individual cases.

An actual measure of the effect of intensity of collecting can be made by considering the numbers of species of molluscs recorded along the Somerset coast. There are two main sources of information—the present survey and Swanton's extensive list (1912).

The numbers of species recorded during the present survey shows a gradual increase seawards. Swanton's records, however, show an enormous peak at Weston—which is the largest town on the banks. He records forty-nine species as against the eleven species recorded during the present survey. His Weston figures are also considerably in excess of the Minehead figures (seventeen species). In view of the gradual increase shown by the records of the present survey a comparison of the fauna records made at different stations is probably valid and will now be made.

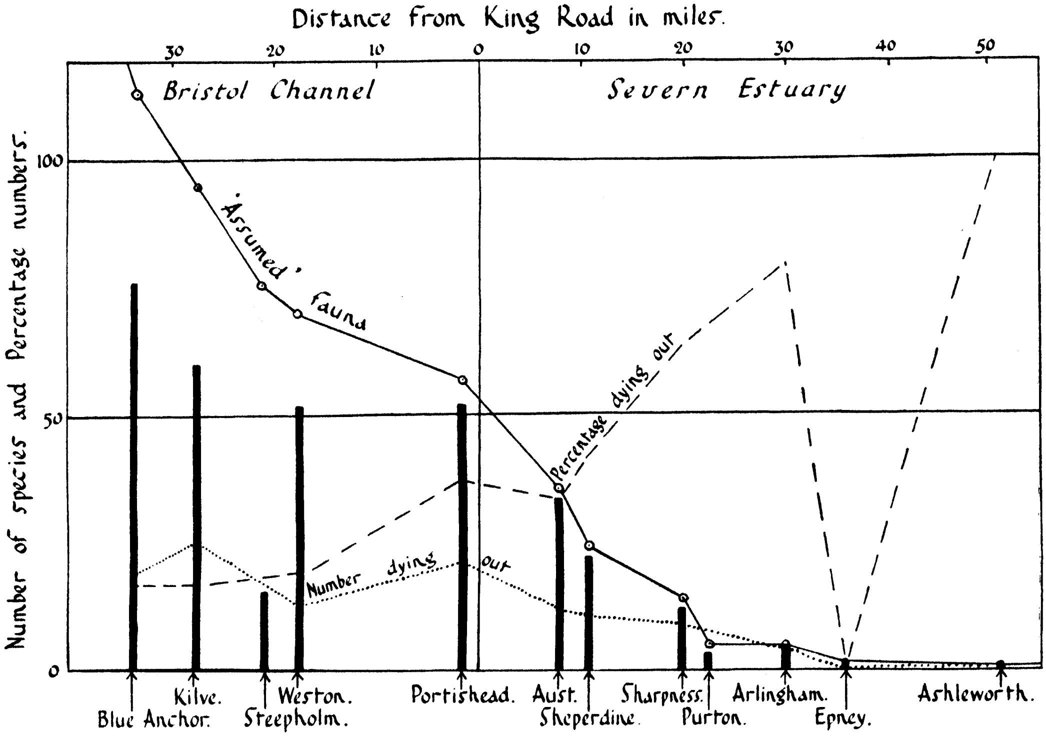

Fig. 10. The numbers of species of marine intertidal animals recorded during the present survey (excluding pelagic forms).

The graph (Fig. 10) is constructed in the same manner as Fig. 9. The discrepancy between the actual number of species recorded and the total 'assumed' population gradually increases in a seawards direction as in Fig. 9. The rise of the assumed population between Portishead and Weston is a measure of the difference in composition of the two faunas, since in actual number of species they are equal. The small numbers of species recorded by Yonge & Lloyd (1938) from Steepholm is in part due to the fact that extreme spring tides were not experienced during the collecting period. None-the-less, of the Weston fauna some thirty species occur above low water of ordinary tides, and although some are sand-living forms there are five or ten species which are missing from Steepholm and present at Weston. It seems possible that this discrepancy is due to the action of the powerful currents to which the shores of the island must be subjected.

One curve in Fig. 10 shows the numbers of species which die out at each station, i.e. species which may be recorded from below the particular station but have not been recorded higher. From this data it is possible to estimate the percentage of the (assumed) population of each station which cannot survive the conditions higher up. These are shown in Fig. 10, and it is apparent that the higher up the estuary the greater is the proportion of the fauna which dies out. Above Sharpness where the fauna is very sparse the percentage figures mean little. Below, however, there can be seen a clear demarcation at Portishead because in the Bristol Channel the numbers dying out constitute about one-fifth of the fauna, whereas above Portishead in the lower reaches of the Estuary the proportion is two-fifths. It seems that the geographical distinction between the Bristol Channel and Severn Estuary has also some biological significance, in that conditions governing the fauna appear to change less rapidly with distance below Avonmouth than they do above (see Fig. 7).

Table 14. *The intertidal fauna (all available records) of the Bristol Channel and Severn Estuary. (Records of planktonic, deep water and netted forms omitted. Records of insects and mites are too sporadic for inclusion)*

	Ilfracombe	Minehead	Blue Anchor	Kilve	Stolford	Burnham	Steepholm	Weston	Clevedon	Portishead	Aust	Sheperdine	Sharpness	Purton	Arlingham	Epney	Elmore	Gloucester	Ashleworth	Haw Bridge	Tewkesbury
PROTOZOA	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
PORIFERA	10	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
COELENTERATA:																					
Hydrozoa	40	—	4	6	3	—	—	3	—	5	4	—	—	—	—	—	—	—	—	—	—
Anthozoa	15	—	3	2	—	—	3	2	—	2	1	—	—	—	—	—	—	—	—	—	—
PLATYHELMINTHES	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
NEMERTINEA*	—	—	1	1	—	—	—	1	—	1	1	1	—	—	—	—	—	—	—	—	—
GEPHYREA	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ANNELIDA:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2†	—	—
Polychaeta	6	—	14	8	2	—	1	12	—	11	3	3	1	1	1‡	—	—	—	—	—	—
CRUSTACEA:																					
Ostracoda	49	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
Cirripedia	1	—	2	2	—	—	1	2	—	1	1	1	1	—	—	—	—	—	—	—	—
Cumacea	4	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Isopoda	9	—	5	5	1	—	2	5	—	7	5	5	4	2	1	—	—	—	—	—	—
Amphipoda	27	—	11	15	3	4	1	9	—	10	7	4	5	2	3	1	1	1	3§	1§	3‖
Decapoda	8	—	3	3	—	1	1	3	—	2	1	1	—	—	—	—	—	—	—	—	—
MOLLUSCA:																					
Gastropoda¶	40	10	13	10	1	11	6	28	16	7	4	4	2	—	—	1‖	—	1‖	3‖	—	—
Lamellibranchia	15	7	4	3	—	22	—	21	3	4	2	2	2	—	—	—	—	—	—	—	—
Polyzoa	50	—	6	6	—	—	—	4	—	3	4	2	1	—	—	—	—	—	—	—	—
Echinodermata	2	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tunicata	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total marine species	279	17	71	65	11	38	15	91	19	53	33	23	16	5	5	1	1	1	1	0	0

* *Lineus gesserensis.* ‡ *Nereis diversicolor.* ‖ Fresh-water species.
† Leeches (F.W.). § Two species of *Corophium*. ¶ Includes chitons and *Dentalium*.

In order to present a general picture of the intertidal fauna of the various stations Table 14 has been constructed and shows the numbers of species of the different groups which occur at each station. Records of deep-water species, planktonic or semi-planktonic forms, and of species taken in nets and kypes have been omitted. Fresh-water species have been little studied, and such records of insects and mites as have been made are too sporadic to have any value to the general survey.

The most important groups are the Polychaeta, Crustacea and Mollusca. All three are represented in the Channel by large numbers of species and they penetrate to Sharpness. Beyond this point molluscs are not found until the fresh-water species appear at Epney, but *Nereis diversicolor* penetrates to Arlingham and an amphipod penetrates into fresh water where two more species of *Gammarus* and two species of *Corophium* are also found.

In the case of the Porifera, Echinodermata and Tunicata the rarity of records is quite certainly due in the Upper Channel to rarity of species. With regard to the Polyzoa and Coelenterata it is believed that additional records could be obtained by more detailed work, particularly in summer, but the lists would certainly not approach the length of the Ilfracombe lists. Among molluscs Swanton's records approach the Ilfracombe figures, and the relative scarcity indicated by records made during this survey is due not only to a lesser intensity of collecting, but to the fact that little work was done on the sand and mud banks where lamellibranchs, in particular, are most likely to occur.

Seasonal changes

Species of *Gammarus* were normally less abundant during winter, and although no geographical restriction was observed, evidence is accumulating to show that the zone of breeding specimens is restricted during winter and that the extremes of the range—particularly at the less saline end—are occupied by non-breeding or immature specimens. After the severe frosts of January 1940, the non-breeding specimens of several species showed certain intersex characters and, in the female, reduced brood plates. A more detailed consideration of these points is given in Bassindale (1942*b*).

As collections were made after the severe frosts of January 1940, it might be assumed that numerous evidences of their effect would have been noted. This was not the case, although some changes were observed. *Lineus gesserensis* disappeared from Sheperdine, where it had been common, and from all other stations seaward of this. Although it reappeared by spring 1941, it was not so abundant. This must mean that it had died out at Sheperdine, for if it had merely migrated down river or deeper into the mud, it would have reappeared in large numbers. *Balanus improvisus* seemed to have been killed off. Only a few living ones were seen, and these were commoner at Portishead and Aust than they were at Weston, Kilve and Blue Anchor. Although not conclusive it seemed as though the specimens at the seaward stations had suffered more than the estuarine ones.

The absence of a marked effect of frost agrees with the findings of Fischer-Piette (1931), who shows that the winter lowering of salinity is much more important than lowering of temperature.

Other faunistic notes

The outstanding feature of interest in the estuary is the abundance, during summer, of the deep-water prawn, *Pasiphae sivado*. It is taken in vast numbers in the hose nets set on the shore at Stolford for taking *Crangon vulgaris*. In the summer months it is frequently more abundant than *Crangon* but is always dead. A single sea horse, *Hippocampus*, was taken in these nets in 1936, and two *Leptocephalus* larvae of the conger eel and one *Maurolicus muelleri* were obtained in 1939. At this same fishing station the mud flats are notable for the abundance of *Hydrobia ulvae*. Nearby at Kilve the occurrence of the deep water form, *Solaster papposus*, at low-water mean, occasioned some surprise as did the occurrence, under quite muddy conditions, not only at Kilve but at Weston, Clevedon and sometimes at Portishead, of colonies of *Sabellaria alveolata*. Weston is peculiar in several ways. *Sabellaria* is common on shingle and there is an abundance of certain species not found commonly elsewhere (*Eurydice pulchra*, *Gammarellus homari*, *Laomedia gelatinosa*), or, as with *Calliopius crenulatus*, only found in abundance at Portishead as well as Weston.

The only nudibranch which occurs commonly in the region studied is *Onchidorus muricata*. It was found at low-water extreme spring tide in October 1941 at Portishead, and comes up to spawn on the shore in spring from Porlock Weir to Portishead.

Occasional specimens of *Cyathura carinata* have been found from Blue Anchor to Sharpness. From the abundance of this form on mud in the Tamar (Spooner & Moore, 1940) it seems probable that its apparent rarity in the Severn is due solely to the absence of collecting on the mud banks.

Interesting systematic features are the discovery at Haw Bridge and Ashleworth Ferry of males of a new species of *Corophium*, the discovery at Kilve of a *Caprella* which does not quite fit existing descriptions, and the widespread presence of a Severn saline form of *Gammarus zaddachi* as well as the fresh-water and saline forms which are recorded from other rivers. In addition, some *Sphaeroma rugicauda*, with their dorsal surface more smooth than normal, were taken at Sharpness, and the somewhat localized beetle, *Eurynebria complanata*, was found at Burnham.

Among mysids the species *Schistomysis ornata* occurs, and the form may prove to be *S. kervillei* which is, as yet, regarded merely as a brackish water variety of *S. ornata*.

There are some absentees from the fauna. Two of these are *Gammarus duebeni** and *G. chevreuxi*, and in addition it is to be expected that work on the mud banks will increase considerably the lamellibranch fauna so far recorded and also show that *Corophium volutator*, as well as *Cyathura carinata*, is considerably more abundant than is indicated in the records.†

SUMMARY

1. A list of the fauna of the southern shores of the Bristol Channel and Severn Estuary and an account of the collecting stations have been presented elsewhere (Bassindale, 1940, 1942*a*).

2. The tidal regime and the salinity and turbidity of the waters have been investigated both in the literature and in the field and the following points elucidated:

(i) The tide range increases from Ilfracombe and Swansea to a maximum at Aust. Thereafter the range diminishes (Fig. 2*A*).

(ii) The maximum range of an extreme spring tide is nearly 50 ft. (Fig. 2*A*).

(iii) Neap tides do not pass Framilode (35 miles) (Fig. 2*A*).

(iv) Good spring tides top the weir at Gloucester, and extreme spring tides affect the river to Upton-upon-Severn (66 miles) (Fig. 2*A*).

(v) Tidal currents increase from Ilfracombe to a maximum in the region of Severn Beach and Aust. Thereafter they are still quite high (p. 8).

(vi) A bore develops above Sharpness on spring tides and travels at a maximum speed of 14 knots and a maximum height of 4·5 ft. to Gloucester (Fig. 28 and p. 8).

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* Subsequently discovered at Porlock Weir.

† *Corophium volutator* is abundant at Weston.

(vii) The turbidity of Severn water is very high and is at a maximum between Aust and Arlingham. It increases in winter and the turbid zone remains in the same reaches at all seasons. Hence the maximum turbidity occurs in more saline water in summer than in winter (Tables 5 and 6, Fig. 3 and p. 8).

(viii) The turbid zone moves up and down with the tide causing a maximum turbidity at high water at Arlingham and at low water at Aust (Table 6).

(ix) The amount of silt in suspension during spring tides is greater than at neaps (Table 7). Hence much silt must rest on the bottom during neaps.

(x) There is more silt in suspension in winter than in summer. Hence some must settle out in spring and rest on the bed during summer.

(xi) The silt in suspension increases with depth (Table 8).

(xii) The increase of silt during springs occurs more in the surface waters than in the already heavily laden bottom waters (Table 8).

(xiii) The silt in suspension during springs could be contributed by the rivers in a few years (p. 14).

(xiv) The fresh-water floods in winter push the brackish water zone seawards (Fig. 7).

(xv) There is no vertical salinity gradient (Table 13).

(xvi) Salt water extends on springs to above Epney and on neaps not so far as Arlingham (Fig. 7).

(xvii) In summer the salinity conditions are stable up to Aust, and the zone of maximum variation is above Sharpness (Figs. 7, 8).

(xviii) In winter the salinity conditions are stable only to Weston, and the zone of maximum variation stretches down to Aust (Figs. 7, 8).

(xix) The twice daily salinity variation at Weston is not more than 1 g./l. and is less than the seasonal variation of 7 g./l. (Fig. 7).

3. The fauna from Ilfracombe to Gloucester has been studied.

(i) The marine fauna is extensive at Ilfracombe and less so from Blue Anchor upstream (Fig. 9).

(ii) The fauna dies out more rapidly above Avonmouth than below (Fig. 10).

(iii) The distribution of *Gammarus* species has been closely studied and little seasonal change was noted. A full account is given in Bassindale (1942*b*).

(iv) A new form of *Gammarus zaddachi* and a new species of *Corophium* have been identified but not described.

(v) The severe frosts of January 1940 had little effect on the fauna (p. 26).

(vi) A geographical, floristic and faunistic account of each collecting station is given in Bassindale (1942*a*).

(vii) Notes on the fauna are given (p. 26).

4. A comparison of physical conditions in the Severn and Tees will appear in the May 1943 volume of the *J. Anim. Ecol.* and other comparisons are in course of preparation.

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A STUDY OF THE VEGETATION OF SEA-CLIFFS IN NORTH CORNWALL

By IAN HEPBURN

(*With Plates* 1, 2 *and one Figure in the Text*)

It is well known that cliffs, which are above the reach of high tides, but exposed constantly to sea spray, support a characteristic vegetation of halophytes, most of which are also typical plants of salt-marshes. The composition of the cliff vegetation varies, however, a good deal in different districts of the British Isles and has not often been described in much detail. The present study has been undertaken with a view to gaining some information about the vegetation of 'spray-washed cliffs' in a part of the British Isles where non-halophytic species, such as the arctic-alpines found on the north-west cliffs of Scotland and elsewhere, seem to be mostly absent, and the vegetation can be looked upon as reasonably typical.

The area which was selected for study is situated about half-way down the north Cornwall coast and consists of the strip of coast-line starting at Trebetherick Point, on the east side of the Camel estuary near Polzeath, round Pentire and Rumps Points, and then eastwards as far as Kellan Head (see Fig. 1). The length of this coast-line is approximately 8 miles (13 km.). Less detailed observations have also been made at various points on the west side of the Camel estuary as far west as Bedruthan Steps, and also some miles eastwards in the neighbourhood of Tintagel. These more distant observations have not revealed any new features in the general vegetation, and confirm the presumption that the area studied is typical of a long strip of coast. One of the advantages of the portion of coast chosen is that it is very much indented and actually furnishes examples of all aspects between south-west and south-east, though the general aspect is north.

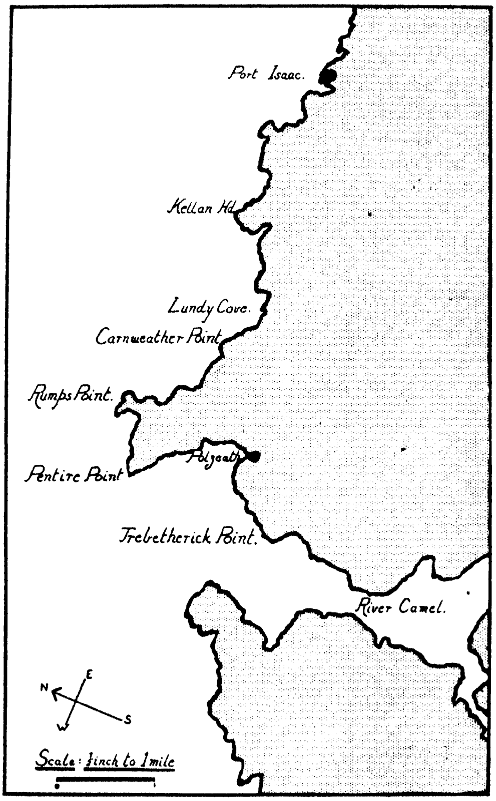


Fig. 1.

The cliffs are mostly composed of Upper Devonian Slate, often showing purple or green bands. There are, however, various igneous intrusions of Diabase or of Pillow lava (Greenstone). The Pillow lava occurs principally round the Pentire peninsula, but Rumps

Point is chiefly Diabase, as is also the stretch from Carnweather Point to Lundy Cove. Though the vegetation occurring on each of these types of rock was studied in the course of the inquiry, there was no evidence of there being any difference connected with the nature of the rock except that the slate generally was more weathered and had thus produced better cracks and pockets for plants to establish themselves in. The cliffs in the whole area are much broken, and rarely consist of more than about 30 m. of bare rock and often of much less, descending to sea-level at Polzeath and Lundy Cove. Above the bare rock, the grassland characteristic of the cliff-tops ascends in varying gradients to an average height of about 60 m. above the sea at the top, where the ground usually becomes comparatively level (Pl. 1, phot. 1).

A number of strips of cliff along this stretch of coast were selected for study. The lengths of these strips were rather varied, largely owing to the difficulty of approaching them. There were, in fact, considerable stretches of cliff which were quite inaccessible (Pl. 1, phot. 1). On the average, the strips studied were from 30 to 40 m. long, and provided a large enough number of plants for their relative frequencies to be estimated with sufficient accuracy.

VEGETATION

It was found that the phanerogamic vegetation does not generally begin until at least 6 m. above the high-water mark along these exposed cliffs, though along the low cliffs bordering the upper reaches of the Camel estuary (not in the area studied), where rough seas cannot occur, typical cliff plants are found growing just on the high-water mark (Pl. 1, phot. 2). Where the rocks approached the perpendicular and possessed few pockets or ledges, they were often completely bare for as much as 20 m. It was also noticed that the more protected the habitat was from wind and weather, the lower the vegetation began. Thus on north- and north-west-facing cliffs, even on rocks with a comparatively slight slope, the vegetation is typically very thin. It is on the east side in this particular area that the vegetation is generally found to occur lowest. This is presumably due to the cliffs with an easterly aspect being protected from the prevailing westerly winds, and probably also to the protection afforded by the northward turn of the cliffs on the east side of Port Isaac bay, which would act as a breakwater when the sea is running from this quarter.

The vegetation of the lower portions of the cliffs is always very open, which means that there are plenty of suitable spaces for colonization which are not occupied. On the flatter portions of the rocks considerable accumulations of soil were often noticed in the cracks which had not been colonized. This soil had presumably originated partly from decayed lichens and previous sea plants, though much of it had probably fallen from higher up the cliffs. The soil always contained a large amount of humus and sometimes a certain amount of sea sand.

It is obvious that the colonization of this habitat does not take place at all readily. The plants which are found growing there are nearly all perennials, generally with long woody roots, and the majority of the plants seen are old and well-established specimens. The difficulty of colonizing must be due to two causes; first, the effect of an excess of salt which is more than the young seedlings can tolerate, and secondly, to the great exposure of this habitat to the strong Atlantic winds and the consequent desiccation produced in a very shallow soil. The effect of the salt is dealt with more fully later. The exposure factor must also be a powerful influence, since the shallow soil must dry quickly, and until the plant has developed its long roots it is likely to suffer frequently from an acute shortage of water. It is, in fact, not unusual to find quite large *Armeria* plants withered up in a dry summer. The amount of water in the soil is, of course, closely connected with the concentration of salt in the soil water. This point is also dealt with more fully later, when the question of salt tolerance is discussed. Apart from this effect of exposure, powerful winds have a marked restraining influence on all vegetation, and this is well illustrated by the very stunted nature of most of the plants occurring in the cliff grassland above the rocks.

In describing the general vegetation of the rocky parts of the cliffs it will be convenient to divide it into an upper and a lower zone. There is actually no sharp division between these zones, and species which are most characteristic of the upper one are frequently met with lower down. It was, however, found in general that certain species were usually seen growing lower than others, and on most cliffs it is possible to distinguish between a lower purely rock zone, whose angle is generally steep, and an upper zone, where the rocks are more broken, the slope frequently less, and having a great deal more soil, largely derived from the cliff-tops, mixed up with it. Owing to the great differences in the height above high-water mark where the vegetation begins, the more obvious and simple method of fixing the zones by their height above the sea is not of much value. As a very rough average, the lower zone can be said to begin about 10 m. above high-water level and to extend from 6 to 15 m. upwards. The upper zone may be only about 3 m. in height or may be as much as 15 m. high, before it joins up with the grassland on the top of the cliffs.

Lower rock zone

The flora of the lower zone is a very restricted one and consists of only about a dozen species. In such a very open community it is hardly possible to speak of a dominant, but there can be no question that *Armeria maritima* is by far the most abundant species and it was present in all the strips studied. It was noticeable that other species, which were common generally, were quite often absent from large suitable areas of the cliffs. For instance, *Crithmum maritimum*, the most characteristic plant of the cliffs, was completely absent from two of the strips studied. It was not found possible to connect the absence or occurrence of species in this community with any obvious factor. In the following list of the species found in this zone, the number of areas where they occur out of a total of 15 possible areas is shown, and also the average relative frequency of each species *in the areas where they were found* is indicated by the usual 1–5 notation:

Occurrence out of 15		Frequency	Notes
15	Armeria maritima	5	Generally growing lowest
13	Crithmum maritimum	4	
13	Spergularia rupicola	4	
9	Beta maritima	3	
8	Atriplex glabriuscula (A. babingtonii)	3	
7	Inula crithmoides	3	
12	Asplenium marinum	4	In shady cracks
9	Plantago coronopus	2	—
8	Limonium binervosum	2	—
8	Cochlearia anglica	2	Generally preferring damp rocks
7	Plantago maritima	2	—
4	Matricaria maritima	4	Very prolific when it occurs
3	Silene maritima	1	Rarely grows at low levels

These thirteen species may be considered as characteristic, but in addition, a number of 'casuals' from higher up the cliffs such as *Sedum anglicum, Erodium cicutarium, Sonchus oleraceus* and a number of others, were found to have gained a foothold occasionally. The only species from above which were found established in any quantity were *Agrostis setacea,* the dominant grass of the cliff grassland, and *Anthyllis vulneraria.*

This study is not intended to give an account of the lichen population, but there are three species which are so ubiquitous in this zone that they can hardly be passed over. These are:

Xanthoria parietina
Ochrolechia parella
Ramalina siliquosa

All three of these occur abundantly in both zones, the first two generally beginning slightly below the phanerogams, though well above the high-water mark, and the last becoming commoner higher up. Other lichens which were noticed in and just below the lower zone were:

Lichina confinis
Anaptychia fusca
Physcia tenella
Lecanora (Placodium) muralis

Upper zone

The upper zone was easier to study because it was more accessible from above and it was possible to survey longer stretches at one time. The most characteristic plants of this zone besides *Armeria maritima,* which is still the most common species, are *Silene maritima,* which frequently covers considerable areas and is largely responsible for this zone looking different from the lower one, *Plantago coronopus,* and *Sedum anglicum. Cochlearia anglica* is also much commoner in this zone. On the other hand, *Crithmum maritimum,* while remaining common, is less frequent. *Daucus gummifer* and *Anthyllis vulneraria* are very regular inhabitants, and also, as might be expected, *Agrostis setacea,* the dominant grass of the cliff-tops. The vegetation as a whole is distinctly thicker than in the lower zone, but it is still generally very open and the composition is more variable. A certain number of the cliff-top plants mix with the vegetation in this zone, though in remarkably small numbers. In the following list the frequencies are indicated rather roughly using the 1–5 notation.

	Frequency
Armeria maritima	5
Silene maritima	5
Sedum anglicum	5
Plantago coronopus	5
Agrostis setacea	4
Crithmum maritimum	3
Cochlearia anglica	3
Beta maritima	3
Atriplex glabriuscula	3
Daucus gummifer	3
Spergularia rupicola	3
Limonium binervosum	2
Inula crithmoides	2
Asplenium marinum	2
Anthyllis vulneraria	2
Matricaria maritima	1
Plantago maritima	1
Cotyledon umbilicus	1

The chief 'casuals' that were noted were *Erodium cicutarium, Leontodon hispidus, Rumex acetosella, Jasione montana, Sagina subulata,* as well as many others.

The same three principal lichens as in the lower zone were universal, but *Ramalina siliquosa* now becomes decidedly the commonest and *Xanthoria parietina* thins out considerably. *Lecanora muralis* and *Physcia tenella* still occur generally, and in addition *Ramalina subfarinacea* is common. On the bare soil near the top of rocks, considerable amounts of *Cladonia subcervicornis* were noticed.

Halophytes in the cliff grassland

Above the rock zones, as soon as the slope eases off sufficiently, a closed association of grassland characteristic of the cliff-tops appears. This is dominated by *Agrostis setacea*, and generally consists of a fairly close sward containing a large number of herb species which are usually more or less stunted. Though plenty of spray must blow across the whole area during high winds, few of the halophytes characteristic of the rocks can compete successfully in this habitat. There are, however, frequently great amounts of *Armeria* in the turf, though this is often very stunted. *Plantago coronopus* is also usually present in large quantity. *Silene maritima* is frequent and *Spergularia rupicola* occasional, but none of the other true cliff species are found. *Sedum anglicum* is common and *Anthyllis vulneraria* frequent, but though both occur on the rocks they are not cliff plants. The maritime species thin out quickly as the distance from the sea increases and *Armeria* was rarely seen in the grassland more than about 300 m. from the edge of the cliffs.

The grassland on the cliff-tops generally consists of a narrow belt, sometimes sloping upwards steeply and sometimes nearly level, varying in width from about 50 m. to over 300 m. from the cliff edge. It usually terminates in a dry stone wall which divides the grass from the arable land behind. Good crops of cereals and roots grow within 100 m. of the edge of the cliffs in many places, and the only crops which seem to suffer from spray and exposure are potatoes.

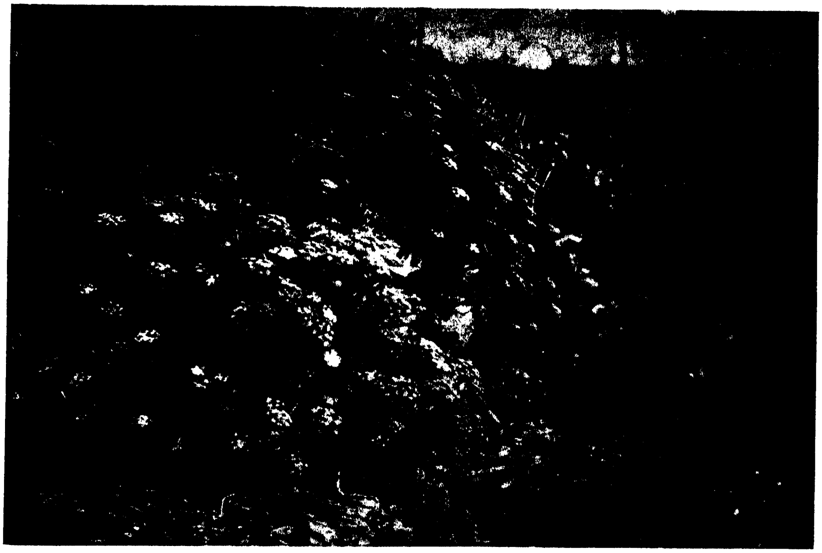
Vegetation on the cliff walls

The dry walls referred to above provide a rather similar habitat to the cliffs themselves, since they are still exposed to a considerable amount of spray, despite the fact that their height above sea-level is anything from 30 to 80 m. In the absence of competition from turf growing species, many of the typical halophytes of the rocks are found well established in the walls associated with other non-halophytic species. Pl. 2, phot. 3 shows the position of a typical cliff wall on the west side of Pentire Point. It was noticed that the walls facing west and north-west, the quarter of the prevailing winds, were much more fully colonized with halophytes than those with an east or north-east aspect. On west-facing walls, halophytes were seen in plenty up to as much as 400 m. from the cliff edge, but rarely much farther inland, whereas on east-facing walls about 100–150 m. from the cliff edge seemed to be about the limit. Pl. 2, phot. 4 shows a west-facing wall which was nearly 400 m. from the edge of the cliffs, but had gently rising ground all the way to it from the sea. It is thickly colonized with *Armeria maritima* and also contains much *Silene maritima*. Provided that there are no obstacles and the intermediate ground has a regular slope, when there is a strong wind and a high sea running considerable amounts of spray undoubtedly blow inland for at least half a mile, and in lessening amounts probably considerably farther. This can be well appreciated by observing the heavy deposits of salt on the windows of houses standing on the rising ground behind Polzeath Bay, which faces west.

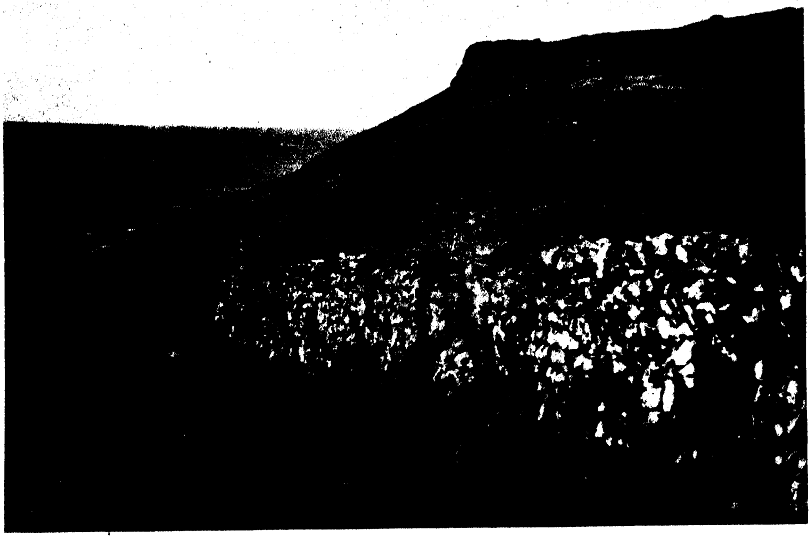
The relative frequencies of species in the walls vary greatly, In the following list of the main species observed in these walls, only rough average frequencies are given:

Armeria maritima	a.	Daucus gummifer	f.	
Silene maritima	a.	Cochlearia anglica	o.	But absent from large stretches
Agrostis setacea	a.	Asplenium marinum	o.	In shady cracks
Plantago coronopus	f.–l.a.	Anthyllis vulneraria	o.	
Spergularia rupicola	f.	Beta maritima	r.	
Sedum anglicum	f.	Crithmum maritimum	r.	Only two plants seen

Phot. 1. General view of north-facing cliffs on the Pentire peninsula during a rough sea.



Phot. 2. *Crithmum maritimum* growing just above high-water level along the cliffs of the upper Camel estuary.



Phot. 3. A typical west-facing cliff wall, showing its position in relation to the cliff grassland and the sea.

Phot. 4. A west-facing cliff wall nearly 400 m. from the cliff edge, thickly colonized by *Armeria maritima* and *Silene maritima*.

The principal species not previously noted in quantity on maritime rocks were as follows:

Cotyledon umbilicus	f.–l.a.	Sonchus oleraceus	o.
Thymus serpyllum	f.	Convolvulus arvensis	o.
Senecio jacobaea	f.	Cerastium vulgatum	o.
Leontodon hispidus	f.	and many other cornfield weeds	

The lichens, *Ramalina siliquosa* and *Ochrolechia parella*, still persist in great quantities, the stones of some west-facing walls being almost completely covered with the former. *Xanthoria* is, however, almost entirely absent. The other most common lichen noticed was *Ramalina subfarinacea*, and often large amounts of *Parmelia trichotera*.

In comparison with these cliff walls, those a little farther inland, which are out of range of the halophytes, were found to support a very mixed collection of wall plants and cornfield weeds of which the following species are the most typical:

Sedum anglicum
Cotyledon umbilicus
Senecio jacobaea
Digitalis purpurea
Leontodon hispidus
Dactylis glomerata
Festuca ovina
Sonchus oleraceus
Convolvulus arvensis
Cerastium vulgatum
Rubus spp.
Cirsium spp.
and many other cornfield weeds

Vegetation of rocks not exposed to sea spray

With a view to obtaining some more information about the importance of the salt factor, a search was made for habitats which were apparently similar to the cliff habitat except that they were not exposed to sea spray. These were provided in a number of small disused quarries which occur along the tops of the cliffs, generally facing in the opposite direction to the sea. Though most of these were situated within 400 m. of the sea, their aspect precluded any appreciable quantities of salt from reaching them. Owing to their proximity to the cliffs some of the species which are typical of the cliffs naturally appear there also, but a number of other plants which seem to be definitely excluded from areas which are exposed to spray occur in addition. These form rather a mixed collection and most of them are found also in the cliff grassland. Of the plants found in this habitat which also occur on the cliffs exposed to spray, few are true halophytes, these presumably being excluded by an insufficiency of salt. The following list gives the principal species found:

Plants also found on cliffs exposed to spray		*Plants excluded from areas exposed to spray*	
Sedum anglicum	a.	Teucrium scorodonia	a.
Silene maritima	f.	Cotyledon umbilicus	a.
Plantago coronopus	f.	Erica cinerea	f.
Agrostis setacea	f.	Calluna vulgaris	f.
Sagina subulata	f.	Dactylis glomerata	f.
Armeria maritima	o.	Festuca ovina	f.
Jasione montana	o.	Brachypodium sylvaticum	o.
Leontodon hispidus	o.	Senecio jacobaea	o.
Plantago maritima	r.	Digitalis purpurea	o.
Cochlearia anglica	r.	Thymus serpyllum	o.
		Parietaria officinalis	o.
		Rubus spp.	o.
		Asplenium trichomanes	o.
		A. adiantum-nigrum	o.

The areas studied were not sufficiently extensive for the above list to be considered as very complete.

DISCUSSION OF RESULTS

Summary of field observations

The foregoing observations show up certain facts, which may be summarized as follows:

(1) There is only a small community of plants which can survive the exposure to strong winds and a large amount of spray on the lower cliffs.

(2) On the higher parts of the cliffs where there is a good deal more soil, less exposure to spray, but the same exposure to wind, certain other plants are found to occur. All the plants found in the lower zone occur here also, though in rather different relative amounts.

(3) Above the rocks, in the cliff grassland which forms where the slope is such that a deeper and more stable soil is present, very few of the true cliff plants can compete with the grasses and the numerous other members of this grassland community.

(4) Higher up still, on the dry walls bordering the cliff grassland, there is a habitat somewhat similar to that which obtains on the cliffs proper. This has an exposed aspect but not much exposure to spray, and possesses a dry soil. Here a number of the true cliff species reappear, competition with the grassland species being removed.

(5) A number of other species are found growing in habitats which appear to be similar to the cliff rocks, but which are not exposed to salting or to particularly high winds.

Salt factor

It is clear that the plants which grow in the lowest zones must be able to tolerate rather wide ranges of salt in their root water and solutions of considerable strength upon their leaves. Also, since the places where they grow are restricted in most cases to positions where they are to a greater or less extent exposed to spray, it is probable that they require some salt for their normal growth. As has already been pointed out, they are nearly all perennials producing long woody roots or a mass of fibrous roots, and possess either fleshy leaves or a well-developed hairy protection. After a storm, followed by a drying period, it is not unusual to find salt crystals on the foliage. The leaf development is, of course, a protection against desiccation as well as salt.

Any accurate estimations of the concentration of salt in the root water are impossible for two reasons. First, it is very difficult to obtain a sample of soil which is at all representative from the inside of narrow cracks in the rocks. The difficulty is not merely mechanical, for in addition it is difficult to decide exactly where samples should be taken when the roots are sometimes several feet long. Secondly, the variations in the salt concentration, at any rate near the surface, must be very considerable. After a big sea has been running, the concentration of salt in the surface soil may approximate to that in sea water, but a period of quiet may follow the storm and, being exposed to sun and light breezes, the salt content in the soil water will tend to rise. On the other hand, heavy rain may occur immediately after or during the storm, with a consequent fall in the salt content. There may be therefore more variation in the salt concentration than in a salt-marsh, where the roots frequently become actually immersed in sea water, and dehydration will generally be less rapid. At the same time, owing to the great length of the roots of many of the cliff species, their water supply will mostly be derived from soil well below the surface where the variations in the salt content are not likely to be so great. The figures quoted below, which were all obtained from specimens of soils taken from near the surface, show probably a greater variation in the salt concentration than actually occurs in the root water of most of the cliff plants.

At all times of the year and particularly during the summer, there must be quite long periods when little or no salting occurs, though even during fine weather strong Atlantic swells are frequent. Furthermore, high winds and heavy rain are very frequently associated with each other, and the effect of one will often be immediately counteracted by the effect of the other. The average annual rainfall for the district is about 35 in. (at Trebetherick), but this will not have such a large effect in keeping the salt content of the soil down during the growing period of most of the plants since a large proportion of the rain falls during the four months from October to January (16 in. average).

The following are some results of salt contents obtained from soils collected from round the roots of the lowest growing *Armeria* plants. It was only possible to collect the soil from near the surface. In each case the soil was collected in a corked bottle and the amount of water determined by evaporation in an oven at 110°. The amount of salt in the dry sample was then determined by extracting a weighed quantity with water and titrating the solution against *N*/100 silver nitrate solution with potassium chromate as indicator. The results were then expressed as the percentage of salt in the soil water. Specimens were collected under different atmospheric conditions and three different samples were taken for each set of conditions (numbered 1, 2 and 3).

	% of salt in soil water		
Conditions when collected Sample ...	1	2	3
During a storm (dry day)	2·5	2·1	2·0
After 24 hr. heavy rain	0·65	0·50	0·37
After 3 days' dry weather following a storm	3·4	2·7	2·5

These results show rather a wide variation between the specimens taken under the same conditions, due to the differences in depth and in exposure of the various samples taken. They do, however, establish the considerable leaching out of salt by rain, and the increase in salt content of the surface soil, at any rate after dry weather. It is rather surprising that a higher percentage of salt was not found in any of the 3rd lot of samples.

Higher up the cliffs, the salt content probably never becomes very great, though in the upper rock zone it may be considerable. A few results are given below, which confirm this. The analyses were all carried out with soils collected in dry weather, which would mean that the soil water contained the greatest quantities of salt, since no rain had fallen between the last high wind and the time of collecting. Two samples from each zone were analysed.

	% of salt in soil water	
Locality Sample ...	1	2
Upper rock zone	1·3	0·85
Lower parts of the cliff grassland	0·55	0·35
Typical north-west-facing cliff walls	0·45	0·35

All the above samples were obtained in exposed places, and it is certain that the salt content will be considerably less in many other parts of these zones.

Absorption of salt by non-halophytes

It is well known that halophytes take up considerable quantities of salt into their structure. It was thought that it might be of interest to ascertain whether plants which are found growing in places exposed to spray, but which are not usually classified as halophytes, also took up much salt. Specimens of *Anthyllis vulneraria* which were found on the cliffs, for instance, appeared to possess more fleshy leaves than when growing away from the sea. Accordingly specimens of three species, *Agrostis setacea*, *Anthyllis vulneraria*, and *Matricaria maritima* were collected from exposed places on the cliffs and were then ashed in a muffle furnace at 800°. A weighed quantity of ash was in each case extracted with water, and the solution was then titrated with *N*/20 silver nitrate solution. The following results were obtained:

Species	% of salt in ash
Matricaria maritima	24·7
Anthyllis vulneraria	13·5
Agrostis setacea	2·6

These results show that all three of these species take up some salt, and must possess considerable salt tolerance, though the result for *Agrostis* is surprisingly lower than the others. Only *Matricaria maritima* can be called a seaside plant, and even it would hardly be classed as a halophyte. Some further work on the salt contents of other cliff plants will be carried out, since this method promises to give some interesting information.

It is clear, however, that none of the above preliminary investigations give any very definite information about either the salt tolerance or the salt requirements of spray-washed plants. The difficulty of obtaining representative soil samples removes most of the value of data from soil analyses, though possibly some more investigation might furnish rather more information. There is another possible method of approaching the question of salt tolerance, which might yield some more definite results, and it is proposed to make a start on some experiments on the following lines. Prof. Tansley has suggested that specimens of cliff plants might be grown in a garden plot and that the effect of spraying these with varying amounts of salt water of different strengths could be observed over a considerable time. This could be combined with an analysis of the plants themselves in order to ascertain the amounts of salt absorbed under different conditions. It is likely that the degrees of tolerance vary considerably for different species and this method, if successful, might give some useful information both on this point and as to which of the species actually require salt.

Rock growing plants not tolerating spray

In connexion with the list of plants which were found growing on the quarry walls and which were not found on the exposed cliffs, there is another factor which ought to be considered, namely the degree of acidity of the soil. The soil found on the cliff-tops is a very light and stony one, which contains on the average at least 25% of humus. The average *p*H was found to be 5·2. It is, therefore, a very suitable habitat for such plants as *Calluna vulgaris*, *Erica cinerea*, *Teucrium scorodonia*, *Jasione montana*, etc. The soil found in the quarry walls was of approximately the same *p*H. But the average *p*H of the soil in the cracks of the exposed cliff rocks in the lowest zone was found to be 6·8, whilst in the upper zone, though more variable, it is generally higher than in the grassland and was found to be 5·7 on the average. In several cases in the lowest zone the *p*H was found to be 7·0, and the soil, which was rich in humus, contained sufficient calcium carbonate to give a vigorous evolution of gas with hydrochloric acid. It is clear that a certain amount of sand has been thrown up by wind and waves and has lodged in the cracks in the rocks. The sand particles are, in fact, in many cases quite visible amongst the humus. The sand in the neighbourhood is peculiarly rich in calcium carbonate, that at Polzeath containing about 60%, whilst at Harlyn Bay, on the west side of the Camel, it contains more than 80%. For this reason, sand at the present time is being transported in large quantities from the Camel estuary for agricultural purposes. It is obvious that the presence of this calcium carbonate in the soil, producing a nearly neutral *p*H, would by itself be sufficient to account for the absence of *Calluna, Erica, Teucrium, Digitalis*, etc., from the lower places on the cliffs. On the other hand, the higher rock zones do not receive much sand, except when near a beach, and the soil remains strongly acid. Since, with the exception of a few casual specimens of *Jasione montana*, none of these typical calcifuge plants were observed growing in the higher cliff zone to which they could have easily spread from above, it would seem that they could not tolerate salting either. A much more typical wall species which appears to be largely excluded from spray-washed localities is *Cotyledon umbilicus*. This species grows profusely on walls in the neighbourhood where the soil is largely derived from sea-sand and contains over 30% of calcium carbonate. Other excluded species which are not also calcifuge are *Parietaria officinalis*, *Festuca ovina*, *Dactylis glomerata*, etc., and the ferns, *Asplenium trichomanes* and *A. adiantum-nigrum*. None of these species has been observed on the exposed cliffs, but they are frequent inhabitants of the quarry walls and exposed rocks farther inland.

Plants peculiar to cliffs exposed to spray

The majority of the true cliff plants noted are also typical inhabitants of salt-marshes. There are, however, a few species which seem to be more or less confined to the cliff habitat. Of these, *Crithmum maritimum* is obviously the most characteristic. *Limonium binervosum* is also a distinct species which appears to be largely confined to the rocks, but is found sometimes elsewhere on shingle beaches and on mixed sand and shingle which is occasionally visited by high spring tides. *Spergularia rupicola*, at any rate in this neighbourhood, seems to be confined to the cliffs, since in the salt-marshes farther up the Camel estuary it is *Spergularia salina* and occasionally *S. marginata* which are found. *Daucus gummifer* and *Sedum anglicum*, though never salt-marsh plants, have a wider range than the cliffs and can hardly be included in this list.

Since *Limonium* and *Spergularia* are both represented by closely allied species which are common salt-marsh plants, and the fern, *Asplenium marinum* is sometimes found a considerable distance from the sea, there remains only *Crithmum* as a species which is peculiar to the cliff habitat. Further study may show what characteristics of cliffs which are exposed to spray are specially suited to the requirements of this species, but at present it is not clear why it should be absent from both salt-marsh and shingle-beach communities.

In conclusion, the author would like to express his thanks to Prof. R. C. McLean and Dr Mackenzie Lamb for kindly determining the lichens, to Mr A. Constant for drawing the map, and to Prof. A. G. Tansley for much help and advice.

REVIEWS

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This number contains 8 original papers, 4 reviews, and 113 Notices of Publications on the Animal Ecology of the British Isles. Surveys of the animals living in small bodies of freshwater are few for this country, and this enhances the usefulness of Miss E. M. O. Laurie's account of the fauna of a non-acid pond on the hills of North Wales. It contained areas of *Equisetum limosum*, *Potamogeton natans*, *Scirpus palustris*, and *Sparganium minimum*, and quantitative collections of animals living in these and other habitats were made at different seasons. At least 98 species were found. Miss Gwendolen Rees reports an analysis of parasitic worm egg counts on some North Welsh hill pastures, which shows that a drained and carefully managed field, sown with good grass and clover, carried fewer worm eggs from sheep droppings than a rough unimproved pasture. The chief infestation of the sheep occurs in winter, and the greater infestation on poor pasture is attributed to lower resistance of the sheep. J. M. Winterbottom, in a study of the bird fauna of an area in Northern Rhodesia, presents further evidence of fluctuations in tropical bird population. He also discusses how far census methods and comparative counts are practicable for judging the relative compositions and densities of tropical and temperate bird faunas. In his survey, 152 species of birds were recorded in 539 days' observation, on a 1100 acre area—originally woodland, now cleared and cultivated except for some scrubby grassland and some trees and a swampy stream.

C. H. Mortimer and E. B. Worthington place on record some basic morphometric figures for Windermere, and there is a fine photograph of the head of the lake and its surrounding hills. Miss Penelope M. Jenkin gives a very full account of temperature conditions in Windermere, their seasonal changes, the development of a discontinuity layer (whose terminology is discussed), and the classification of the lake in limnological terms. As with Scottish lochs, the seasonal circulation of water vertically is less sudden than in Continental lakes of similar type, and there is a certain amount of circulation throughout the year. The heat budget is described.

There are three population studies of land mammals. F. C. Evans did elaborate live-trapping and marking experiments on the wood-mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*) in a mixed wood near Oxford, for 29 months. Fluctuations were measured, also the occurrence in different types of woodland and ground vegetation. The bank voles appeared to have a higher density in bracken areas. It seemed also that more bank voles survived the population "crash" on low than on high density areas—an interesting suggestion in view of conventional biological ideas about "optimum" habitats.

Charles Elton and Mary Nicholson present a full analysis of fur-trade statistics bearing upon the well-known "ten-year cycle" in populations of the Canadian lynx. This is proved to have been going on for at least 206 years, and to have occurred in a parallel cycle in the last 100 years in many separate regions of Canada, with an average periodicity of about 9·6 years. This evidence, the statistics of which are mostly published for the first time, supports the theory that this Canadian population cycle is partly controlled by climatic influences that are still undiscovered. Dennis Chitty and Mary Nicholson give the sixth annual report of an enquiry into fluctuations in numbers of lemmings, arctic foxes and snowy owls in the Canadian Arctic, and of epidemic diseases among Canadian sledge dog teams, illustrated by some impressive photographs of the northern country. The short cycle is shown to have been rising during 1940–41, with a good correlation between the lemmings and predators in the Eastern Arctic, but no clear one in the Western Arctic.

Reviews deal with the *Journal of Ecology*, the Society's *Biological Flora*; the Northern Ecological Association, and the "Bibliography of key works for the identification of the British Fauna and Flora".

Charles Elton.

THE MYCORRHIZAL RELATIONS OF *PINUS*

(1) **Rayner, M. C.** Mycorrhiza in relation to Forestry. *Forestry*, **8**, 96, 1934.

(2) **Rayner, M. C.** Mycorrhizal associations in Scots Pine. *Forestry*, **9**, 154, 1935.

(3) **Rayner, M. C.** The Mycorrhizal habit in relation to Forestry. II. Organic composts and the growth of young trees. *Forestry*, **10**, 1, 1936.

(4) **Rayner, M. C.** The Mycorrhizal habit in relation to Forestry. III. Organic composts and the growth of young trees. *Forestry*, **13**, 19, 1939.

(5) **Rayner, M. C.** and **Levisohn, Ida.** The Mycorrhizal habit in relation to Forestry. IV. Studies on mycorrhizal response in *Pinus* and other Conifers. *Forestry*, **15**, 1, 1941.

The publication of the last of the above papers has brought the work of Dr Rayner to a point at which a general review may be appropriate. It may be recalled that the work originated in coniferous plantations on Wareham Heath, which gave generally poor and irregular results. Evidence was obtained which suggested that the general failure of the plantations was associated with failure of mycorrhizal development, and a detailed investigation of the problem was, therefore, undertaken.

The papers deal mainly with the mycorrhizas of *Pinus*, observations being recorded on *P. sylvestris*, *P. laricis*, *P. pinaster* and *P. contorta*. Evidently somewhat similar effects may occur in *Picea*, *P. sitchensis* and *P. abies* and in *Cupressus lawsoniana*. It is implicit in the treatment that suitable mycorrhizal relations are necessary for satisfactory growth in *Pinus*. This assumption is based essentially on the correlation existing between certain morphological and structural types of mycorrhiza on the roots and the maintenance of satisfactory growth rates of the shoots. The conclusions are based on experiments in the field and in pot cultures, which covered a wide range of manurial or other treatment.

In normal or satisfactory mycorrhizal conditions, the roots of *Pinus* bear frequent, short, dichotomously branched laterals of a pale to golden brown colour. The tips and growing regions of these are invested by an external sheath of interwoven mycelium (the *mantle*), and in section they show the penetration of the cortical tissue by an intercellular network of hyphae. It is now generally accepted that some intracellular infection also occurs, which may show considerable variability in extent, but which, if severe, always shows apparent digestion of the invading hyphae.

In untreated Wareham soils, mycorrhizal development is normally poor, the lateral roots being few, the mantle commonly poorly developed or absent. Only one type of satisfactory mycorrhiza has been observed, that due to association with *Boletus bovinus*. The fungus has been isolated from both Scots and Corsican Pine, and from its sporophores which occur in the planted areas. The identity of the cultures from various sources has been proved. The fungus is considered to pass through two main phases in nature. During the summer, it is associated with the tree roots. Each mycorrhizal system lasts for one season and the formation of a satisfactory system in one year by no means ensures a corresponding development during the following growing season. During the winter, *B. bovinus* exists in the soil, apparently mainly or entirely in the form of characteristic rhizomorphs. These are abundant by March but disappear when young root growth is active. The fungus has been isolated in culture from these rhizomorphs and similar rhizomorphs are formed in culture under certain conditions, apparently associated with limitation of nutrient material. The production of sporophores by *B. bovinus* has not been accomplished in culture but it is noticed that in the field, sporophore formation occurs most readily under conditions which permit the development of satisfactory mycorrhizas. At Wareham certain compost treatments (see below) are particularly effective in both respects, while normally, poor mycorrhizal development and a general absence of sporophores are characteristic. The facts, therefore, support Melin's view that *B. bovinus* depends for completion of its growth cycle upon the symbiotic relation. Although most of the detailed cultural work refers to strains of *B. bovinus* in relation to *Pinus sylvestris* and *P. laricis*, the evidence suggests that this fungus can form mycorrhizas on other pines and possibly on other conifers.

In addition to the poorly developed mycorrhizal types, *pseudo-mycorrhizas* may also occur. These are rare or absent in untreated Wareham soils, but they may occur in treated soils. The most characteristic fungus is apparently *Mycelium radicis atrovirens* (Melin). The pseudo-mycorrhizas show slender unbranched lateral roots, often slightly beaded owing to irregularities of growth, and from dark brown to black in colour. The mantle is composed of much coarser hyphae and shows a crusty investment with an appearance of root constriction in section. The cell walls thicken and become brown in colour and there may be extensive intra-cellular infection without evidence of hyphal digestion. This suggests one-sided parasitism of a severe type. The fungus has been isolated and appears to be identical with the Swedish strain. Another form (probably introduced in humus inoculations), *M. radicis nigrostrigosum* Hatch, has also been found in the area. It develops a palisade-like arrangement of hyphae in the mantle. Both these fungi often develop on the mantle formed by other mycorrhizal species.

The marked feature of the Wareham soils when untreated, is, however, their capacity for inhibiting or limiting fungal growth. As a result of this, feebleness of mycorrhizal development is characteristic and severe attacks on roots by fungi are rare or absent.

The first problem attacked, therefore, was that of inducing the development of normal mycorrhizas. As it was possible that scarcity or absence of suitable fungi might be responsible for the usually scanty mycorrhizal development, particularly when exotic species of conifer were planted, experiments were devised to test the effect of adding suitable sources of such fungi to the soil. For this purpose, humus from native or other well-grown forests was added in the vicinity of the planted trees or seeds. When brought from a distance (e.g. Corsica or California) the humus was maintained in a moist and otherwise favourable condition for fungal growth. The effect of this treatment, either in the field or in pot cultures, was to give increased tree growth and to favour the development of normal mycorrhizas. Moreover, as the effects of the added humus were small when it was previously sterilized, it was evident that the effect was due to its microbiological characters and not only to its chemical composition. The improvements produced by humus inoculation proved to be temporary, tending to disappear after the first year. Moreover, when the fungus from the improved mycorrhizas was isolated it proved to be *Boletus bovinus*, already noted as the only prominent mycorrhizal fungus in the area, and probably commonly present in the humus inoculations. It was necessary, therefore, to suppose that the imported strain was in some manner in a better physiological state than that already present in the heath soils. The facts were, however, consistent with the view that the Wareham soils were in some way unfavourable to the maintenance of the best mycorrhizal relations.

In addition to the experiments with humus inoculations, observations were also carried out on the effects of adding organic composts. It was inferred that the Wareham soils contained organic matter poor in nitrogen so that organic composts rich in this element were mainly employed. These composts usually gave increased tree growth. They were of the following types, with *p*H values (1 in 10 water extract) between 6·1 and 6·8. The figures are percentages of dry matter:

		Total N	P_2O_5*	K_2O*	Ash
C_5	Brewery hop waste + dried blood	4·64	2·80	0·75	26·7
C_8	Straw + ammonium phosphate	1·89	2·15	0·63	32·3
C_1	Straw + dried blood	3·33	0·77	1·04	34·0
C_7	Straw + ammonium sulphate	2·25	0·56	0·52	34·4
C_4	Straw + sawdust (50%) + dried blood	2·19	0·28	0·43	20·1

* 'Available' (method not stated).

They contained 1% by weight of the nitrogenous component (e.g. dried blood). The materials were mixed, moistened and allowed to stand under controlled conditions for at least two months. When used the composts were almost indistinguishable in appearance from woodland 'mull'. Of those mentioned above (those for which analytical description is available), C_5, C_8 and C_1 were most successful (in that order) in giving increased tree growth. The others gave amounts of growth only slightly above the untreated controls though the differences are apparently regarded as significant. Softwood sawdust was more effective than that from hardwoods. The improvements given by the three best composts were very striking. After three years, plants from untreated soils remained less than 5 cm. in height in one experiment, while those receiving composts C_5, C_8 and C_1 were over 35 cm. in height (*Pinus sylvestris* and *P. contorta*), or in *Pinus laricis* 20–30 cm. in height. Equally striking was the improvement observed in root development. There was marked stimulation of short root production, the majority of these laterals developing forked mycorrhizas of the structural type characteristic of healthy plants. As there was a very good correlation between these features and the growth of the whole plants, it was concluded that the treatment with suitable composts was primarily important in removing the features of Wareham soil which are inimical to normal mycorrhizal development.

The organic components of the composts were considered to be the chief factor in bringing about this improvement. This was partly because the analyses of available potassium, phosphate and nitrogen did not serve to distinguish the value of the composts very definitely, but also because field experience with mineral manures had apparently not been very successful, though it is stated that phosphatic manures had proved beneficial. Further experiments were carried out in pot cultures in which mineral solutions were used in comparison with composts. In these mineral solutions, the characteristic features of the composts in 'available' nitrogen, phosphate and potash were reproduced. As the example given below shows, smaller increases were obtained when mineral salts only were employed:

Mean weight (*g. per* 100 *plants*), Pinus sylvestris

Treatment ...	Control	C_5 compost	C_5 salts	C_1 compost	C_1 salts
	19·9	171·8	70·6	113·7	32·5

While it is evident that part of the beneficial effect may be due to the increased supply of available ions, known to be at a low level in heath soils, it is considered probable that the organic materials present in the compost also have a large effect. This effect is not removed by sterilization of the compost and is therefore a function of its composition not of its fungal or bacterial flora.

This conclusion is amplified into a more general theory of the way in which the composts are effective. It is assumed that the peaty constituents of the Wareham soil contain a relatively high proportion of cellulose residues and low proportions of residues of the protein or lignin types. A higher protein and lignin content might, therefore, render the substrate more suitable for the mycelia of the mycorrhiza-forming fungi. Apart from the support lent to this view by the effects of adding composts of the required type, it was found to be in harmony with certain other facts. Thus soils favourable to correct mycorrhizal development had their suitability for this purpose reduced when cellulose was added. To some extent also, these assumptions were confirmed by experiments in which humus inoculations were added along with compost treatment. The beneficial effects of humus inoculation then tend to become continuous (over the periods observed) although in the ordinary way they disappear after about a year, presumably owing to the exhaustion of the small amount of suitable organic matter introduced. The importance of the balance of cellulosic to non-cellulosic residues is further emphasized by the observation that in Wareham soils, the addition of cellulose may lead to severe attack by *Mycelium radicis atrovirens*, and to corresponding damage to the health of the pine seedlings.

It is suggested as a basis for this work, that in woodland soils of the raw humus type, a stage of humus decomposition marked by the activity of the mycorrhiza-formers, is related directly with conditions favourable to tree nutrition, the formation of mycorrhizas typical for the tree species indicating a definite phase in the process. With this phase is bound up the evolution of an environment stimulating the production of short roots, and promoting a physiological state both in young rootlets and in the mycelium, favourable to mycorrhiza formation. Rapid accumulation of "duff" or "mor" indicates the onset of changes unfavourable to these activities and thus leads to interference with the development of normal mycorrhizas and to disturbances of nutrition.

As far as the significance of the mycorrhizal relation is concerned, we are left with the choice between two alternatives. A satisfactory mycorrhizal state may be either a *sign* of tree vigour and of a generally favourable soil environment or it may be a *cause* of the increased tree vigour and enhanced shoot growth. It does not appear that there is as yet any decisive evidence which enables us to decide between these two alternatives, although the evidence is not unfavourable to the view that the mycorrhizal relation is advantageous in some respect in nature.

As far as the significance of the organic composts is concerned, the evidence appears to be at present indecisive, although perhaps few ecologists acquainted with the trend of recent work would object to Dr Rayner's general statement, summarized above. One difficulty is that it has been shown elsewhere (Neilson Jones, W., *J. Agric. Sci.* **31**, 379, 1941) that the Wareham soils are inimical to fungal growth, this feature being associated apparently with the presence of sulphides, and hence probably due to anaerobic conditions, presumably the result of long-continued waterlogging in winter. The gradual disappearance of the deleterious effects in pot cultures is in agreement with this suggestion and so also is the fact that the harmful effects appear to be greater in spring. Moreover, the planted areas are said to have benefited greatly in drainage and aeration from tractor-ploughing. It appears, therefore, that the special characters of the soil are likely to be related to prolonged anaerobic phases rather than to those features of the soil organic matter which are common to all heathy or acid-peat soils. The point is not unimportant because the facility with which pines may establish themselves on some acid-peaty soils and their apparent toleration of such habitats, suggests that the high carbon/nitrogen ratio of typical acid peats is not necessarily unfavourable to the normal mycorrhizal relation, if, indeed, this be a requisite for rapid growth of pines. From the purely ecological point of view then, the improvements following compost treatment might conceivably follow upon any or all of four effects: (1) improved aeration of the soil as a result of disturbance and treatment; (2) an altered type of organic matter with lower carbon/nitrogen ratio, for example; (3) increased amounts of available nitrogen, phosphorus, etc.; (4) a reduced hydrogen-ion concentration. [It is noteworthy in the latter connexion (*a*) that the mycorrhizal fungi are stated to be very sensitive to the hydrogen-ion concentration, (*b*) that the *p*H of the composts is high (6·0–6·8), and (*c*) that mineral manures found to be beneficial are basic slag and bone meal, both of which usually increase the soil *p*H.] As no evidence as to the relative influence of these different factors is presented, it seems to be necessary to reserve judgement as to the nature of the effects produced by composts, although the evidence as a whole is not unfavourable to the hypothesis put forward. On the other hand, Dr Rayner's views as to the possible role of the soil organic matter in relation to mycorrhizal fungi are so much in agreement with other lines of enquiry in soil microbiology, that it would be premature to reject them while the evidence remains incomplete. It is evident that in this field, the problems approach a point at which conclusions of great value to ecologists and to practical foresters may be expected.

A general review must necessarily do less than justice to the more detailed aspects of work of this type, which covers a wide series of problems. It is necessary to say, therefore, that these papers are a valuable contribution to the study of the effects of humus inoculation and of compost treatments in forestry; of particular interest is the demonstration of the possible dangers of humus inoculation in introducing undesirable forms of fungi into the area. Thus certain pseudomycorrhizal forms appear to have been introduced in this way in the Wareham area while the possibility of increasing the virulence of such forms in the field by compost treatment has also been demonstrated. Both results offer much scope for further enquiry. The outstanding feature of the whole work is, however, its detailed contribution to our knowledge of the mycorrhizal fungi and the mycorrhizal structures under British conditions. The original papers need to be consulted for the methods employed and for many incidental features of great interest. This is a large and positive contribution to a difficult subject and one upon which its author may well be congratulated.

W. H. P.

A STUDY IN PLANT BIOLOGY

The Reproductive Capacity of Plants. By **E. J. Salisbury.** Pp. 244 + xi, 8 plates and 35 text-figures. London: G. Bell and Sons. 30*s*. net.

It is a biological axiom that if a species is to maintain itself in the natural system, it must reproduce itself at such a rate that each individual is succeeded by at least one survivor among its offspring. This average rate is evidently maintained by the majority of species but it has long been common knowledge that the number of possible offspring vastly exceeds this minimum and there are various well-known examples which illustrate the enormous mortality which does, in fact, take place. In so far as any general opinion can be said to hold, it is probable that the output of seed is considered to be related to the intensity of mortality—a point of view which is perhaps based on the very large seed production of certain specialized species, such as parasites and saprophytes, in which individual seeds may have only a limited chance of survival. It is curious that little recent attention had been given to these points. There were no easily available sources of information and, although the subject lent itself readily to numerical examination, it seemed to have escaped the general tendency in biology towards quantitative and statistical treatment. This omission was the more striking as it was known that the study of the magnitude of the variation in animal numbers (particularly, for example, the fur-bearing animals and rodents) had revealed biological facts of the first importance and had greatly strengthened our knowledge of the mode of action of natural selection. The publication of this book is, therefore, particularly opportune not only because it collects the existing data on seed production in a convenient form, but because it also presents a very large body of original and unpublished evidence in appropriate statistical manner.

The investigation of reproductive capacity in plants is first approached by considering the data for the average weights of seeds and fruits. The results are summarized in tables, each of which represents a group of species characteristic of some general habitat or community type. From the results of the survey, it is shown that with an increasing tendency of the habitat towards shade, there is a parallel tendency towards increasing average seed weight. In a similar manner, plants of closed communities tend to have higher average seed weights than those of open communities. The highest average seed weights among British species tend to be found among the dominants of woodland communities. These relations are illustrated by the following summary, which gives the average weights of all propagules (i.e. fruits and grass 'seeds' included) for species from different types of community:

Community type ...	Open	Closed or semi-closed	Scrub or wood margin	Shade	Shrubs	Trees
No. of species	98	51	50	36	24	20
Average weight (mg.)	1·3	1·9	4·0	11·3	85·4	653·4

The generalizations based on these results can be put in another form, namely, that the larger the supply of food material provided by the parent plant in the seed (or other propagule) the more advanced will be the phase of succession that the species will normally occupy. It need scarcely be emphasized that there are some striking exceptions to these generalizations. Attention is drawn to the special advantages that may accrue to certain sand-dune and shingle beach species by the possession of large seeds, which enable them to develop a large root system at an early stage. Among trees also, *Betula*, *Pinus sylvestris* and *Fraxinus excelsior* are frequent among the colonizing species of woodland, have a high light requirement and are characterized by relatively small propagules. Lastly, as a class, species with characteristic mycorrhizal stages, such as the orchids and Ericaceae, possess extremely small seeds, between 0·001 and 0·0002 mg. in weight. Hence it is suggested that the mycorrhizal condition is biologically important in conferring on the seedlings of such plants, the ability to survive saprophytically, although possessing the minimum of food reserve in the seeds. Two other classes of plant are characterized by seeds of the same order of weight as those of the mycorrhizal types, these being the completely saprophytic and many parasitic species. It may be noted, however, that *Cuscuta* seeds are larger than is usual in this class, but that the seedlings may contain chlorophyll and may live independently for some seven days before a host plant is parasitized. These various lines of inquiry show, therefore, that the weight of its seeds is an important biological characteristic of a species and, usually, it may be related to the mode of life or habitat requirements.

When attention is turned to seed output, expressed as the average number of seeds produced per plant, it becomes much less easy to generalize, this being partly because of the very great range of variation in numbers of seeds. One great difficulty in this type of work is, as the author points out, the determination of the average seed production. It is essential, if the data are to have permanent value, that they should be based on careful estimates in normal habitats, and preferably that they should represent a large sample. In practice, attempts to cut short the labour of counting involved, by examining only a few 'average' individuals almost always give inaccurate results, since it is common to find a population consisting of a few individuals with fair sized fruits and numerous individuals with smaller ones. In such cases the individuals chosen by visual inspection as 'average' are almost always above the average in seed production. In one case given by the author, that of *Agrostemma githago*, the mean seed number for ten capsules was 34·8, while for 165 capsules it was 24·5. No general rule can be given as to the number of individuals which should be examined as this obviously depends on the range of variation shown. In this work, the observed data are given with suitable statistics, the aim being to give an approximation to the seed production of the many, rather than details of the seed production of a few. A very large proportion of the data presented is original and the figures cover a very wide range of species and of field conditions.

The analysis of the results along lines similar to those employed for seed weights, reveals fewer differences. There is, for example, no significant difference between average seed production by species of open, semi-open and closed communities. In these species groups, average seed production ranges widely about the number class yielding 800–1600 seeds per plant. On the other hand, two sorts of habitat yield strikingly and significantly different ranges of seed production. Species of shaded habitats commonly produce around 100–200 seeds per plant, while species of intermittent habitats (such as shingle, coppiced areas in woods and exposed mud) tend to produce very abundant seeds, ranging around 5000–10,000 seeds per plant. The difficulty of comparison here, lies in the overweighting effects of the very large seed outputs in certain species in each class. Thus in the last-mentioned group (of intermittent habitats), the *mean* seed production of the 41 species listed is 28,289 seeds per plant, while for shade species it is only 280 seeds per plant (22 species). In contrast, for 39 species of permanently *open* habitats and for 22 species of *closed* communities, the respective mean seed numbers per plant are 2904 and 1944. It will be noted that all these *mean* numbers lie considerably above the *modal* values for the different groups of species.

Seed output is not, however, the final test of reproductive capacity. This latter is defined as the product of the average seed output (per plant) and a fraction representing the percentage germination of the seeds. It 'should also include an estimate of the rate of vegetative multiplication where this is a significant feature'. Because of the difficulty of estimating this latter factor, the conclusions drawn in this book are based mainly on species in which vegetative reproduction is unimportant and the study of these leads to some interesting and novel conclusions.

Perhaps a typical example is that of the four poppies, *Papaver rhoeas, P. dubium, P. hybridum* and *P. argemone,* which show marked differences in geographical range and abundance. Of these, *P. rhoeas* is the most widely spread in Britain and is more abundant than *P. dubium* which has also a wide geographical range in this country. The other two species are southern continental types, uncommon in Britain, of which *P. argemone* is apparently rather more widely spread, though somewhat local in distribution. Estimates of the mean reproductive capacity of these species are as follows—giving mean values and leaving out the statistics of variation given:

Species	Capsules per plant	Seeds per capsule	Percentage germination	Reproductive capacity
P. rhoeas	12·5	1360	64	10,928
P. dubium	6·83	2008	42	5,757
P. hybridum	7·28	230	91	1,529
P. argemone	6·81	314	63	1,347

The conclusion evident from these figures is that the more widely distributed and more abundant species tend to possess a correspondingly higher reproductive capacity. The conclusion is borne out by numerous other examples. Thus in the case of the three British species of *Scilla, S. nutans, S. verna* and *S. autumnalis,* with strikingly different geographical ranges, the figures given are:

Species	Vice-comital frequency*	Mean reproductive capacity
S. nutans	97·1	102
S. verna	24·7	51
S. autumnalis	4·7	28

* Mean percentage for England, Scotland and Ireland.

We have here then a broad and well-founded generalization which is at variance with the view which has long been accepted, and which was stated by Herbert Spencer. This view assumed that a high reproductive capacity was related to a high mortality, as in the case of many parasites and saprophytes. Thus high reproductive capacity was considered to be, by implication, a form of life insurance in so far as the individual species was concerned, a high premium being required when the risks of mortality were greatest. By contrast, it now appears that high reproductive capacity is a positive biological asset which allows the occupation of a more extensive territory. Further, comparison of annual and perennial species shows that the latter usually have the higher seed output, although the risks of failure in replacement are lower for the perennial than for the annual. Thus the view is taken 'that for most species at least the seed output is considerably in excess of that requisite for mere replacement of losses by death and sufficiently so to bear no obvious relation to the normal seedling mortality. The size of the seed output, or more precisely the reproductive capacity, is regarded as a positive asset in the competitive equipment of the species which tends to ensure occupancy of the available ecological niches and so to ensure the species' frequency and abundance.'

The scope of vegetative multiplication is discussed on somewhat broader lines as it is at present less amenable to detailed quantitative treatment. The point is made that among the most successful of British species are those with a generous seed output and, in addition, some vegetative method of reproduction. In general, however, vegetative multiplication is biologically equivalent to the provision in the seed of a large food reserve and it is therefore not surprising to find, as in the case of the heavier seeds, that species with vegetative multiplication are particularly characteristic either of densely populated habitats, of those which are shaded or of those containing an advanced stage of a plant succession. Thus, methods of vegetative reproduction are biologically important in giving tolerance of competition and in permitting success under competitive conditions. There is, of course, often some alternation between these vegetative methods and ability to reproduce by seeds. Under damp or shady conditions, vegetative multiplication is likely to predominate while seed production is favoured by higher insolation. Similarly, it is shown that in *Lamium galeobdolon*, for example, that the length of vegetative 'runners' may be almost doubled in a wet growing season. There are, however, a few striking exceptions to these generalizations. Thus *Allium carinatum* appears to flower freely in wet seasons but to produce more frequent bulbils in dry seasons. *Allium vineale* occurs in three varieties, of which *A. compactum* produces no flowers but a head of small bulbils, while *A. capsuliferum* has an inflorescence consisting of flowers only. The former is a pestilential weed in dry, sandy fields especially in the Eastern counties, while *A. capsuliferum* is confined to the west and is apparently a plant of damper habitats. Such examples may serve as warnings against too facile generalization.

The preceding paragraphs have indicated the lines of attack upon which the general conclusions have progressed. They give little indication of the wealth of data upon which these conclusions are founded. The investigation of seed output, for example, deals also with the relation of this feature to such possible factors as life span, soil, climate and competition and also with the relation between the number of capsules on a plant and the average seed production in each capsule. Other chapters give detailed studies of reproductive capacity in various special cases. These include parasites and saprophytes, orchids, the genera *Hypericum*, *Gentiana*, *Linaria* and *Verbascum* as well as a mass of data for a great range of British species. If only for the observational data it contains, the book will be indispensable for those interested in plant biology. It is not, however, from this point of view alone that it may be unreservedly commended. It has the merit not only of focusing attention on a neglected field of investigation but of emphasizing the necessity and advantages of studying plants in nature. In this and in its integration from a great range of data it maintains the best Darwinian tradition. Few botanical books of recent years have presented the material for so many generalizations in the field of plant biology or have done this in so broad or so convincing a manner. We may congratulate Professor Salisbury on a notable achievement and his publishers on their enterprise in undertaking such a publication under existing conditions.

W. H. P.

BIOLOGICAL FLORA OF THE BRITISH ISLES

ACCOUNTS PUBLISHED OR IN PREPARATION: JAN. 1943

The accounts already published are:

Juncus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. inflexus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. effusus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. conglomeratus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. subnodulosus Schrank, by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
Zostera L., by T. G. Tutin. *J. Ecol.* **30**, no. 1.
Z. marina L., by T. G. Tutin. *J. Ecol.* **30**, no. 1.
Z. Hornemanniana Tutin, by T. G. Tutin. *J. Ecol.* **30**, no. 1.
Cladium Mariscus (L.) R.Br., by V. M. Conway. *J. Ecol.* **30**, no. 1.
Aster Tripolium L., by A. R. Clapham, W. H. Pearsall and P. W. Richards. *J. Ecol.* **30**, no. 2.
Juncus filiformis L., by P. W. Richards. *J. Ecol.* **31**, no. 1.
Juncus macer Gray, by P. W. Richards. *J. Ecol.* **31**, no. 1.
Rhamnus cathartica L., by H. Godwin. *J. Ecol.* **31**, no. 1.
Frangula alnus Mill., by H. Godwin. *J. Ecol.* **31**, no. 1.

These may be obtained from the Cambridge University Press, 200 Euston Road, N.W. 1, at 1*s.* each. Standing orders for all parts issued may be placed at the reduced price of 9*d.* each.

The following are being prepared:

Acer campestre L. and *A. pseudo-platanus* L., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.
Aconitum anglicum Stapf, H. A. Hyde, National Museum of Wales, Cardiff.
Adoxa moschatellina L., Prof. M. Skene, The University, Bristol.
Allium ursinum L., T. G. Tutin, 1 The Old Abbey, Abbey Road, Cambridge.
Allium vineale L., Miss R. H. Scott, Botany School, Cambridge.
Andromeda polifolia L., Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield.
Asperula odorata L., Dr A. R. Clapham, Department of Botany, Oxford.
Blackstonia perfoliata (L.) Huds., Dr B. Colson, University Department of Botany, Reading.
Carlina vulgaris L., *Cirsium palustre* (L.) Scop., and *C. vulgare* (Savi) Airy-Shaw (=*C. lanceolatum* (L.) Scop.), Dr W. A. Sledge, University Department of Botany, Leeds 2.
Corallorrhiza trifida Chatel., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.
Daphne laureola L., Dr P. W. Richards, Botany School, Cambridge.
Eriocaulon septangulare With., Dr Leighton Hare, Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey.

Galium erectum Huds. and *G. mollugo* L., Miss M. Priestley, c/o Botany School, Cambridge.

Glyceria maxima (Hart.) Holmb., Miss J. M. Lambert, Westfield College, at Oxford.

Goodyera repens R.Br. Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.

Helictotrichon (*Avena*) *pratense* (L.) Pilger, and *H. pubescens* (Huds.) Pilger, G. O. Carson, School of Agriculture, Cambridge.

Juncus articulatus L., em. Wahlenb., and *J. acutiflorus* Ehrh. ex Hoffm., Dr A. R. Clapham, Department of Botany, Oxford.

Juncus squarrosus L., Prof. W. H. Pearsall, F.R.S., University Department of Botany, Sheffield.

Juniperus communis L., T. G. Tutin, 1 The Old Abbey, Abbey Road, Cambridge.

Leontodon leysseri (Wallr.) Beck (*Thrincia hirta* Roth.), Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Leucojum aestivum L., Dr F. B. Hora, University Department of Botany, Reading.

Limosella aquatica L., Dr F. W. Jane and Miss R. Dowling, Department of Botany, University College, Gower St, London, W.C. 1.

Limosella subulata Ives, Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Linum anglicum Mill., and *L. catharticum* L., Dr P. W. Richards, Botany School, Cambridge.

Listera cordata (L.) R.Br., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Lloydia serotina (L.) Rchb., and *Lobelia dortmanna* L., Dr N. Woodhead, University Department of Botany, Bangor, N. Wales.

Luzula forsteri (Sm.) DC., and *L. pilosa* (L.) Willd., Prof. T. M. Harris, University Department of Botany, Reading.

Melandrium dioicum (L.) Simonk. and *M. album* (Mill.) Garcke, H. G. Baker, Hosa Research Laboratories, Windmill Road, Sunbury-on-Thames, Middlesex.

Myosotis arvensis (L.) Hill, *M. collina* Hoffm., and *M. versicolor* Sm., A. E. Wade, National Museum of Wales, Cardiff.

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Narthecium ossifragum (L.) Huds., Dr Mollison, University Department of Botany, Old Aberdeen.

Polygonum persicaria L., etc., N. Simmonds, Botany School, Cambridge.

Quercus robur L., and *Q. petraea* (Mattuschka) Liebl., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.

Rhynchospora alba (L.) Vahl, emend. Ait. f., and *R. fusca* (L.) Ait. f., Miss E. Canton, Department of Biology, Technical College, Sunderland.

Rumex spp., J. E. Lousley, 7 Penistone Road, Streatham Common, S.W. 16.

Scilla non-scripta (L.) Hoffmanns. & Link, G. E. Blackman, Imperial College of Science, London, S.W. 7.

Sonchus asper (L.) Hill, and *S. oleraceus* L., emend. Hill, R. A. Lewin, c/o Botany School, Cambridge.

Subularia aquatica L., Dr N. Woodhead, Department of Botany, Bangor, N. Wales.

Tamus communis L., I. H. Burkill, F.L.S., Clova, The Mount, Leatherhead.

Tilia cordata Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.

Trientalis europaea L., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Urtica spp., P. Greig-Smith, Botany School, Cambridge.

Valeriana officinalis L. and *V. sambucifolia* Mikan, J. Carpenter, c/o Botany School, Cambridge.

Viburnum lantana L. and *V. opulus* L., Dr H. Godwin, Botany School, Cambridge.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account singly or in collaboration, should communicate with Dr A. R. Clapham, Department of Botany, Oxford, or with the Hon. Secretary of the Society.

COLORATION OF ACHENES IN *SONCHUS*

It has been observed that the achenes of *Sonchus asper* Hill, exhibit at least four well-marked varieties of colour, two of which occur in abundance in parts of Scotland, while at least one has been found in 1943 in England. It is suspected that the differences, which are apparently combined with similar variations in achene width, may be genetical, but as their incidence seems, in this country, to be correlated with latitude it would be extremely interesting to obtain further information on their respective distributions.

Briefly, the varieties of colour are

(1) The typical brown, which, in the stages before maturity, is bright yellow.
(2) A pale fawn variety, lacking the yellow stage in its development.
(3) A white variety, lacking both the yellow stage and the final darkening.
(4) An olive variety, in which a green coloration is soon superimposed on the yellow.

It is possible that similar varieties occur in *S. oleraceus* L., but no records have so far been found.

Samples of achenes of these species, from all parts of the British Isles, and especially from Scotland, would be welcome and extremely useful additions to a collection which is at present very inadequate. Ripe fruits from a single capitulum, packeted and marked with locality, date, and the colour of unripe achenes on the same plant, should be sent to the address below, together with any observations that may be of interest; the more dates and localities represented, the better.

It would also be interesting to know whether any of these varieties occur outside the British Isles.

Ralph A. Lewin,
c/o The Botany School,
Cambridge

BIOLOGICAL FLORA OF THE BRITISH ISLES

L. C. (Ed. 11) No. **1891**

Juncus macer S. F. Gray (*J. tenuis* auct. mult. non Willd.)

P. W. Richards

Sect. Poiophylli. A rather weak perennial, very variable in stature. Leaves 10–25 cm. long, nearly all basal, from a very short upright rootstock, narrowly linear, channelled, with a broad sheathing base which is prolonged above into obtuse scarious auricles several times as long as wide (Fig. 1). Flowers in a loose, rarely compact, terminal panicle which is much exceeded by at least one of the very narrow leaf-like bracts. Perianth segments narrowly lanceolate, very acute, greenish, becoming straw-coloured, 3–4 mm. long. Capsule ovoid, obtuse, mucronate, shorter than the perianth.

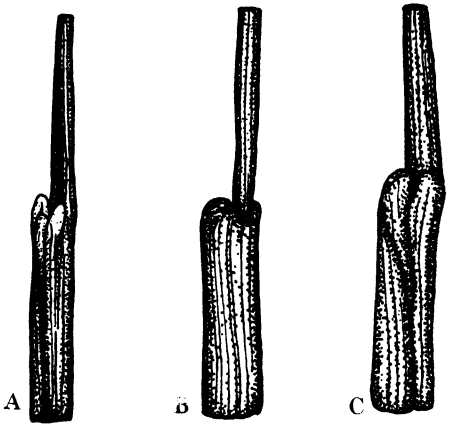

Fig. 1. Auricles of the leaf sheath in *Juncus macer* S. F. Gray and *J. dudleyi* Wiegand. A, *J. macer* (High Bentham, Yorks. Leg. A. Wilson, August 1917). B and C, *J. dudleyi* (St John River, Fort Kent, Maine. Leg. O. W. Knight, 10 August 1905). From specimens in the Cambridge University Herbarium. ×4.

A very distinct species, in Britain varying very little except in size. A plant of North American origin, probably introduced in the British Isles (except possibly in south-west Ireland) and characteristic of paths and road margins on acid base-deficient soils. In North America it is much more variable in its characters, especially in the form of the inflorescence, and also occupies a wider range of habitats.

The closely related *J. dudleyi* Wiegand (distinguished from *J. macer* by its taller, more stiffly erect habit and by the leaf bases having firm brown auricles (Fig. 1) which are broader than long) was found on marshy ground by the roadside at Crianlarich, Perthshire, by C. E. Salmon in 1915 (spp. in Herb. Kew and Brit. Mus.). It has since been refound in the same district (Simpson). *J. dudleyi* is also an American species and is doubtless introduced in Britain: it has been found as an alien in Thuringia (Hegi, 1906, p. 173). Ecologically it differs (in America) from *J. macer* in preferring basic, or at least neutral, soils (Fernald, 1930, p. 367).

I. *Geographical and altitudinal distribution.* Local in Great Britain as far north as Invernesshire and the Outer Hebrides, but still spreading. In England and Wales present in many west and south coast counties and frequent or abundant in some districts (e.g. Merioneth and parts of Caernarvonshire, southern Lake District): absent in most of the east coast counties from the Thames to the Tweed, and in most midland and north-eastern counties. In Scotland found in most of the south-western counties, also in Midlothian (83), Stirling (86), Perth (87–9), Angus (90), Kincardine (91), South Aberdeen (92), West Inverness (97), Argyll (98), Dumbarton (99), Clyde Isles (100), North Ebudes

(104) and Outer Hebrides (110). In Ireland abundant in South and North Kerry (1 and 2) and West Cork (3), also recorded for Clare and Aran Islands (9), Wicklow (20), Down (38) and Antrim (39). The spread of the species seems to be taking place from more than one centre and mainly in a west to east direction (see X), but its present distribution seems to be determined partly by its avoidance of districts with predominantly basic soils and possibly also by a slight preference for regions of high rainfall.

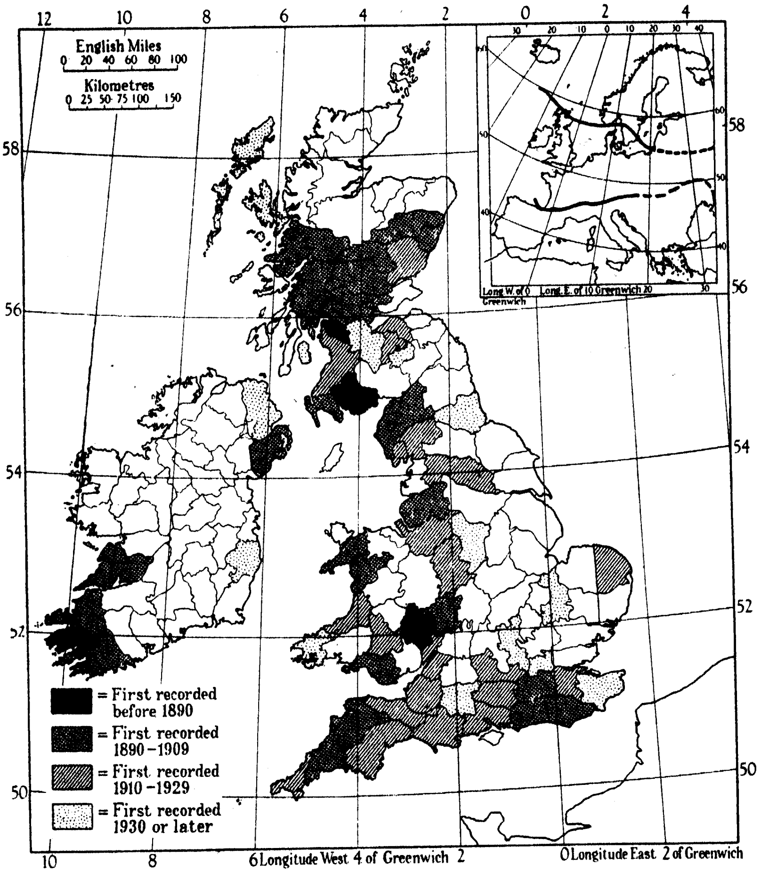
12
10
8
6
4
2
0
2
4
English Miles
0 20 40 60 80 100
Kilometres
0 25 50 75 100 150
58
56
54
52
50
= First recorded before 1890
= First recorded 1890–1909
= First recorded 1910–1929
= First recorded 1930 or later
Long. W. of 0 Greenwich
Long. E. of 10 Greenwich 20
10
8
6 Longitude West 4 of Greenwich 2
0 Longitude East 2 of Greenwich

Fig. 2. *J. macer* S. F. Gray: vice-comital distribution and dates of first records in the British Isles, and (inset) approximate European limits.

Throughout North America from Newfoundland to Vancouver Island, and from the Peace River southwards to Mexico, Arkansas and Florida: also in south Brazil, Argentina and (doubtfully) south Chile.

Introduced into continental Europe, where it was first observed in 1824, and is now widely distributed from France and north Italy to Jutland, Bohus and Småland in Sweden and eastwards to Bohemia, Hungary, the Middle Dnieper, upper Volga, Volga-Don, Crimea, Caucasus and Transcaucasia in the U.S.S.R. (History of its spread in Europe under X.) Introduced also in China (Meyer sp. in Herb. Kew), Madeira, the Azores, the Cape Verde Islands, Tristan da Cunha, Australia and New Zealand.

In Britain mainly at low altitudes, but at 900–1000 ft. (275–300 m.) near Loch Laggan

Hotel, west Inverness (sp. in Herb. E. S. Marshall). To 800 ft. (244 m.) in Glen Esk, Angus (Corstorphine). To 500 m. in mountains of Silesia (Graebner, 1934, p. 115). To 4200 ft. (1280 m.) in California (Jepson, 1923–5, p. 202): at 5500 ft. (1700 m.) at Hot Springs, Colorado (Jones sp. in Herb. Brit. Mus.), and at 6000–8000 ft. (1800–2400 m.) at San Luis Potosi, Mexico (22° N. lat.) (Parry and Palmer sp. in Herb. Kew).

II. *Habitat.* The usual habitat is on the edges of roads, along paths and cart-ruts and along rides in woods. It is apparently intolerant of closed vegetation; thus along a roadside near Loughrigg Tarn, Westmorland, there is a well-marked zone at the edge in which *J. macer* is abundant (see III), but farther towards the ditch where the open vegetation is replaced by a closed turf of *Nardus*, *Juncus squarrosus*, etc., *J. macer* stops abruptly. On paths through grass fields it only occurs where the traffic is sufficient to wear bare patches in the turf. The preference of the plant for roads and paths is no doubt partly due to its method of seed dispersal (VIII (*h*)), but is probably also due to a positive preference for compacted soil, such as also appears to be shown by certain other 'viatical' species (cf. Bates, 1935). The habitats are usually moist throughout the summer and damp or with pools of standing water in winter.

It generally, if not always, grows on slightly acid, more or less base-deficient soils of clayey, loamy or gritty texture. On the roadside near Loughrigg Tarn, Westmorland, where *J. macer* is abundant, the *p*H was 6·4 (colorimetric). At Angley Woods, Cranbrook, Kent, it grows on soil with a *p*H of about 6·9 (colorimetric). No other *p*H measurements are available.

The habitats are often quite unshaded, but it tolerates considerable shade. In Alderholt Wood, Dorset, it grows in "dense shade" on the edges of drains (E. W. Jones).

In south-west Ireland it is not confined to roadsides, but has been found by Praeger in natural habitats, e.g. on shores and islets of lakes at Cloonee, Kerry (Praeger, 1934, p. 312), on salt-marshes on the island of Inishmore in Galway Bay (Praeger, 1934, p. 165). Scully (1889, p. 336) found it "on a small grassy flat within a few yards of the sea, and quite near such maritime plants as *Carex distans*, *C. extensa*, *Juncus gerardi*, etc.; the latter were within tidal influence, while *J. tenuis* was just outside its reach".

On the continent of Europe its habitats are similar to those in Great Britain, and there too it is characteristic of roadsides, paths and woodland rides. In Germany it occurs chiefly on firmly trodden, usually grassy, paths on clay or peat, more rarely on sand, also rarely with other adventives near mills, where it is not persistent (Graebner, 1934, p. 115). E. W. Jones says of its habitats in France and western Germany: "Always in woodland rides or felled areas on damp or heavy soil of base-deficient character."

In North America it is also principally a plant of paths and roadsides, but, as already mentioned, it occurs in a wider range of habitats than in Europe. In the Chicago area it is "common along roadways and paths. Always to be found on soils that are packed by travel" (Pepoon, 1927, p. 216), but Harshberger (1911) records it for dunes on the Isle aux Sables, Lake of the Woods (p. 400), prairies on the Wisconsin drift (p. 524) and in wet meadows (p. 541).

III. *Communities.* Generally a constituent of open (seral) road- and pathside communities (but see above). The following list from a moist unshaded roadside near Loughrigg Tarn, Westmorland, is probably typical: *Agrostis tenuis*, *Cynosurus cristatus*, *Euphrasia* sp., *Juncus macer*, *Leontodon autumnalis*, *Poa annua*, *P. pratensis*, *Plantago major*, *Polygonum hydropiper*, *Potentilla procumbens*, *Prunella vulgaris*, *Ranunculus acris*, *Rumex crispus*, *Taraxacum* sp., *Trifolium repens*, *Veronica serpyllifolia*. This community was an open one, and the spaces between the higher plants were mostly filled with bryophytes: there was no single dominant species.

On a slightly shaded path on compacted loam at Angley Woods, Cranbrook, Kent, *Juncus macer* forms part of the following community: *Agrostis* sp. d., *Anthoxanthum odoratum* f., *Calluna vulgaris* r., *Carex ovalis* r., *Galium saxatile* r., *Hypochoeris radicata* o., *Juncus bufonius* l.f., *J. macer* l.f., *Pedicularis sylvatica* v.r., *Plantago major* f., *Poa annua* l.a., *P. pratensis* f.?, *Potentilla erecta* o., *P. procumbens* (?) o., *Prunella vulgaris* o., *Ranunculus reptans* o., *Sieglingia decumbens* f., *Trifolium reptans* l.f., *Veronica serpyllifolia* r. The composition of this community is remarkably similar to that at Loughrigg Tarn, considering the difference in the two habitats.

In Alderholt Wood, Dorset (E. W. Jones, notes made in 1937), *Juncus macer* occurs on Tertiary clay, mainly on hard, partly bare ground on rides, but also in dense shade in the wood proper on the edges of drains. In the rides the associates included: *Alchemilla arvensis*, *Ajuga reptans*, *Cardamine flexuosa*, *Callitriche* sp., *Centaurium umbellatum*, *Fragaria vesca*, *Juncus bulbosus*, *Lysimachia nemorum*, *Potentilla erecta*, *Prunella vulgaris*, *Veronica officinalis*, *V. serpyllifolia*, *Viola riviniana* (?). The flora of the wood proper included: *Pteridium aquilinum* v.a., *Rubus* spp. f.-a., *Lonicera periclymenum* a., *Blechnum spicant* r., *Dryopteris dilatata* r., *Sanicula europaea* o.-f., *Euphorbia amygdaloides* r.; also *Scabiosa succisa*, *Fragaria vesca*, *Ajuga reptans*, etc. *Molinia coerulea*, *Rhamnus frangula*. and *Calluna vulgaris* were present locally.

On the continent E. W. Jones has found *Juncus macer* on oakwoods on clay-with-flints and Tertiary beds, but it is usually a constituent of roadside and path communities. Braun-Blanquet (1928, p. 312) considers it a characteristic species of the *Cyperetum flavescentis* in central Europe.

IV. *Response to biotic factors*. Evidently very resistant to trampling by man and animals, rolling by wheels, etc., and doubtless also resistant to cutting and grazing. Graebner (1934, p. 116) observed that when the plant is trampled down on paths, the rootstock remains obliquely prostrate and the regeneration shoots develop on two sides, instead of all round; the plant thus becomes fan-shaped and the rootstock elongated.

V. (*a*) *Gregariousness*. Does not form extensive stands like those of many other Junci, but grows in small tufts consisting of a single plant: when very abundant many of these tufts may be in lateral contact, so that it may form a more or less continuous zone by the roadside. Often very variable in abundance from year to year.

(*b*) *Performance in various habitats*. Strikingly variable in size and when in flower from 10 to 60 cm. high, but usually 15–35 cm.: possibly this great variability may be partly due to some plants flowering in their first summer. Succeeds in flowering even in deep shade (Graebner, 1934, p. 115).

(*c*) *Effect of frost, drought, etc.* No information.

VI. (*a*), (*b*) *Morphology*. Like *J. squarrosus*, it is a rosette plant bearing mainly radical leaves and has a short upright rootstock, not a creeping rhizome. The latter is normally under 2 cm. long (cf. V (*b*)) and bears upwardly directed lateral buds in the axil of the prophyll and lower leaves: these buds give rise to lateral shoots, and thus the plant comes to have a tufted habit. Each shoot generally bears six leaves, a two-keeled prophyll, usually followed by two scale leaves with very small laminae and then by the foliage leaves which are narrow and channelled. The root system of the adult plant consists of a dense conical mass, 10 cm. or more long, of tough, sinuous, adventitious roots ending in numerous much-branched rootlets. The root hairs are not persistent.

(*c*) *Mycorrhiza.* No information.

(*d*) *Perennation.* Semi-rosette hemicryptophyte. Erect shoots die down completely in the winter (Westmorland, 1941–2), leaving rosettes of green leaves.

(*e*) *Vegetative reproduction.* May occur to a slight extent by the growth and breaking up of the tufts, but probably unimportant.

(*f*) *Longevity.* Perennial, but probably short-lived. Graebner (1934, p. 116) found on the continent that both in the botanic garden and in the wild state it tends to die away after a few years, but the length of life was variable, depending on the habitat: in very wet or shady habitats the plants almost always died after their second year, but in moderately wet places the tufts reached a much greater diameter and several years' growth could be recognized.

(*g*) *Age at first flowering.* Suspected of sometimes flowering in its first year, but no definite information.

(*h*) *Frequency of seed production.* Sets seed in abundance every year.

(*i*) *Ecotypes.* No definite information. The difference in its range of habitat in Europe and America suggests, however, that in Europe only one ecotype may be present (except possibly in south-west Ireland), while in America there may be more than one ecotype.

VII. (*a*), (*b*) *Phenology.* Near Loughrigg Tarn, Westmorland, the rosettes appeared to be just resuming growth on 22 March 1942 (but this was a late spring).

(*c*) Main flowering season late June to August in north Wales and northern England (but flowers not yet open on 22 June 1942 at Cranbrook, Kent); flowering may, however, continue sporadically, probably till the first frosts. According to Graebner (1934, p. 118), flowering, as in many other Junci, is in distinct 'pulses', which are, however, certainly to some extent dependent on weather conditions. The flowers open between 7 and 8 a.m.; most of them close again by midday, but some may remain open till the late afternoon.

(*d*) Fruit ripe from July to September, some capsules continuing to ripen till the onset of winter. Seed may remain in the capsules probably till the following spring.

(*e*) No information as to time of appearance of seedlings under British conditions, but Graebner (1934, p. 118) says that when possible the seeds germinate immediately they are shed, and may do so while still attached to the capsule by their mucilaginous covering.

VIII. (*a*) *Mode of pollination.* By wind. The flowers are very slightly protogynous. In the early morning the ripe stigmas are already visible through the partly translucent perianth of the unopened flower bud. The anthers begin to dehisce about an hour after the flower opens; dehiscence is completed between 9 and 10 a.m. (Graebner, 1934, p. 118).

(*b*) *Pollinating insects.* No records of insect visitors.

(*c*) *Cleistogamy.* Not recorded.

(*d*) *Apomixis.* Almost certainly amphimictic.

(*e*) *Vivipary.* True vivipary does not occur, but see VII (*e*).

(*f*) *Hybrids.* None known.

(*g*) *Amount of seed.* Nine capsules from near Loughrigg Tarn, Westmorland, gave an average of 268 seeds (range 87–348).

(*h*) *Dispersal.* Dry seeds 0·35–0·5 × *c.* 0·2 mm. The outer layer of the testa becomes mucilaginous and swells enormously on wetting, the seeds often forcing the capsule open.

During rainy weather the large slimy transparent masses of seeds resembling frog's spawn adhere to the dehisced capsules. The seeds are readily dispersed by the feet of men and animals, and also by cart wheels and car tyres. The greatly accelerated spread of the species in Britain during the present century (cf. X), like that of another recently introduced viatical species, *Matricaria matricarioides* (= *M. suaveolens*) (cf. Salisbury, 1932, p. 252), may be largely due to the development of motor transport, the 'tread' of the tyres being very suitable for the dispersal of the seeds. The plant is said also to be spread in fodder, and it has been suggested (Bennett, 1897, p. 32; Ridley, 1930, p. 668) that it first reached this country from America by this means.

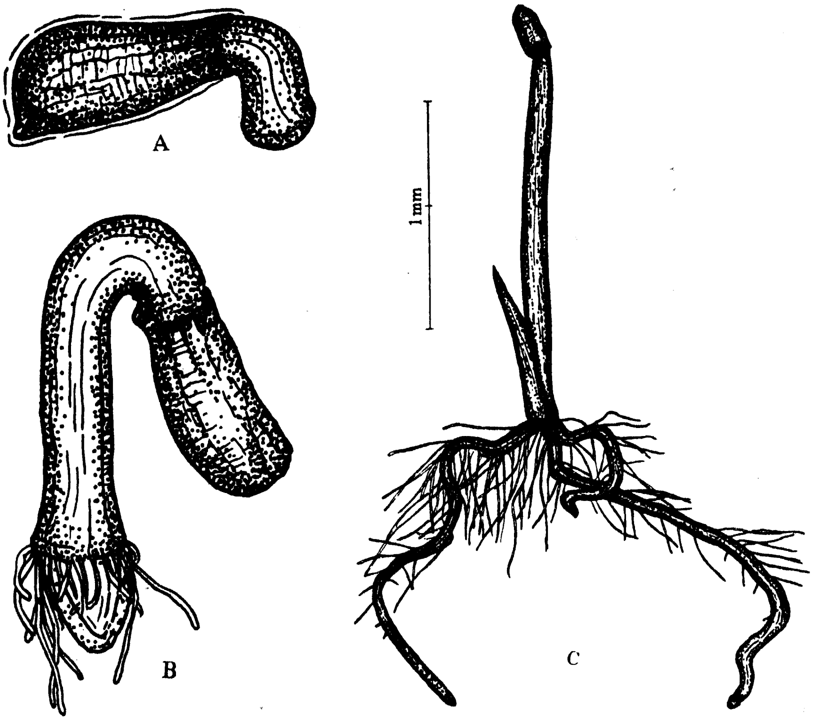

Fig. 3. Three stages in germination of *Juncus macer*. Seeds from Ulpha, N. Lancs, sown in laboratory. A, × *c*. 60; B, × *c*. 60; C, × 30.

(*i*) *Viability*. Seeds stored under dry conditions remain viable for at least 2 years.

(*j*) *Germination*. Germinates only in the light when grown on moist filter-paper under laboratory conditions.

(*k*) *Morphology of seedlings*. See Fig. 3. The seedlings are very similar to those of *Juncus effusus*, etc.

(*l*) *Effective reproduction*. Mainly by seed.

IX. *Parasites, diseases*. None recorded.

X. *History*. The first record of *J. macer* (under the name of *J. gracilis* Sm.) as a British (and European) plant is as follows: "Found by Mr G. Don in 1795 or 1796, by the side of a rivulet in marshy ground among the mountains of Angusshire, but very rarely... we received from Mr Dickson, some few years before the above date, a specimen not so far advanced towards maturity, of what seems to us the same species" (Smith, 1810,

t. 2174). The plant is also said to have been reported from the same locality by D. Don (Hooker, 1821, p. 108), and specimens of undoubted *J. macer*, labelled as collected in the Clova (or Angusshire) mountains by G. Don, exist in various herbaria. In the Herb. S. H. Bickham (Cambridge University Herbarium) there is a specimen labelled "Clova, 1831, G. Don": it bears another label, "*Juncus Gesneri* a synonym of *J. macer* 1831, Mr Jas. McNab". There must be a mistake here as G. Don died in 1814.

After this there was no published report of *J. macer* in this or any other British locality till 1884 when Towndrow (1884) reported finding a single tuft in a "rough and rushy pasture" at Cradley in Herefordshire. Subsequently two earlier records came to light: *J. macer* had been found in Renfrewshire in 1863 (Ewing, 1892), and there is said to be a specimen from Perthshire in Herb. Ansell collected before 1844 (Rep. B.E.C. 1921, p. 401). In 1887 *J. macer* was found in Kirkcudbright (McAndrew, 1887), in 1889 in south Kerry (Scully, 1889) and in 1890 in Caernarvonshire (Lloyd Williams, 1896). Since that date it has been found in new vice-counties almost yearly, and it has become clear that it is a rapidly spreading species. Though it has probably by no means reached its maximum range even now (1942), it seems, as mentioned above, that its further spread is partly limited by ecological factors.

The following is a complete list of the vice-counties in which *J. macer* has so far been found, together with the dates of discovery, as far as they can be traced. In some cases only the date of first publication of the record is known. The name of the first finder is given when different from that of the first recorder:

West Cornwall (1), 1929, H. S. Thompson (Rep. Wats. B.E.C. 1929, p. 36); East Cornwall (2), 1894 (Graham, 1894); South Devon (3), 1929, Gambier-Parry (Rep. B.E.C. 1929, p. 139); North Devon (4), 1895 (Hiern, 1895); South Somerset (5), 1926, Downes (sp. in Herb. Kew); North Somerset (6), 1914, E. P. Sandwith (White, 1914); South Wilts (8), 1936, Gullick (Rep. B.E.C. 1937, p. 510); Dorset (9), 1914, Green (White, 1914); South Hants (11), 1910 (Rayner, 1910); North Hants (12), 1928, Talbot (Rep. B.E.C. 1928, p. 762); West Sussex (13), 1907, Salmon & Hilton (Bennett, 1915, p. 410); East Sussex (14), 1906, Druce & Davy (Druce, 1906); East Kent (15) (Druce, 1932); West Kent (16), 1925, Marriott (Rep. B.E.C. 1925, p. 899); Surrey (17), 1901, Beeby (Salmon, 1931); Middlesex (21) (Druce, 1932); Berks (22), 1916, Monckton (Rep. B.E.C. 1916, p. 505); Bucks (24), 1931, Basden (Rep. B.E.C. 1931, p. 671); East Norfolk (27), 1920, Cobbe (Rep. B.E.C. 1920, p. 151); Cambs (29), Foggitt (Bennett, Salmon & Matthews, 1930); West Glos (34), 1914, Todd (Rep. B.E.C. 1914, p. 75); Hereford (36), 1884 (Towndrow, 1884); Worcs (37), 1909 (Towndrow, 1909); Staffs (39), 1923 (Reader, 1923, p. 279); Glamorgan (41), 1903, Riddelsdell (Rep. B.E.C. 1903, p. 27); Brecon (42), 1927, Gilmour (Rep. B.E.C. 1927, p. 421); Pembroke (45), 1931 (Alston & Sandwith, 1932, p. 238); Cardigan (46), 1924, Todd (Rep. B.E.C. 1924, p. 600); Merioneth (48), 1898, Jones (Salmon, 1910); Caernarvon (49), 1890, Lloyd Williams & Painter (Lloyd Williams, 1896); Derby (57), Todd (Rep. B.E.C. 1937, p. 510); Cheshire (58), 1913, Bailey (Rep. B.E.C. 1913, p. 500); South Lancs (59), Mason, 1904 (sp. in Herb. Kew); Mid-West Yorks (64), 1917, Wilson (Rep. B.E.C. 1917, p. 251); Durham (66), 1935 (Heslop Harrison, 1935); Westmorland and Lake Lancs (69), 1914, Adamson & Pearsall *ex* F. A. Lees (Rep. B.E.C. 1914, p. 75); Cumberland (70), 1906 (Drabble, 1906); Kirkcudbright (73), 1887 (McAndrew, 1887); Wigton (74), Traill (Bennett, 1905); Ayr (75), 1910, Ewing (Rep. B.E.C. 1910, p. 598); Renfrew (76), 1863, Thomson (Ewing, 1892);

Lanark (77), 1933, MacKechnie (Rep. B.E.C. 1933, p. 545); Peebles (78), 1912 (McAndrew, 1912); Selkirk (79) (Druce, 1932); Midlothian (83), 1908, McAndrew in Herb. R.B.G. Edinburgh; Stirling (86), 1894, Somerville in Herb. R.B.G. Edinburgh; Perth (v.c. not stated), before 1844, M'Intyre in Herb. Ansell (Rep. B.E.C. 1921, p. 401); West Perth (87), 1903, Armitage (Bennett, 1915, p. 410); Mid Perth (88), 1908, Ewing (Bennett, 1915, p. 410); East Perth (89), 1903 (Barclay, 1904, p. 59); Forfar or Angus (90), 1795 or 1796?, G. Don (Smith, 1810, t. 2174), 1917, R. H. & M. Corstorphine; Kincardine (91), 1903 (Traill, 1903, p. 251); South Aberdeen, 1894 (Traill, 1897, p. 28); West Inverness* (97), 1896, Grant (Bennett, 1897); Argyll (98), 1902, Ewing (Salmon, 1910); Dumbarton (99), 1891, Watt (Bennett, 1895, p. 39); Clyde Isles (100), 1933, MacKechnie (Rep. B.E.C. 1933, p. 545); North Ebudes (104) (Heslop Harrison, 1936, p. 301); Outer Hebrides (p. 110), 1936 (Campbell, 1936, p. 314).

Ireland: South Kerry (1), 1889 (Scully, 1889); North Kerry (2), 1898, Scully (Praeger, 1901); West Cork (3), 1894 (Phillips, 1894, p. 205); Clare (9), 1895, O'Kelly (Colgan & Scully, 1898); Wicklow (20), 1933, Brunker; Down (38), 1899, Stewart (Praeger, 1938); Antrim (39), 1939, Simpson.

Apart from Don's record, which so long antedates any other, the facts would suggest that *J. macer* was introduced into the British Isles, presumably from America, during the nineteenth century. The introduction may have taken place several times over in different places, as the dates of its first appearances suggest that it has spread from more than one centre, e.g. Herefordshire, north Wales, south-west Scotland. G. Don's record is generally believed to be an error, though apparently confirmed later by his son D. Don: as with some of his other reputed discoveries, he may have given a wrong label to specimens obtained from abroad and cultivated in his garden. This seems the more probable, as the habitat (if accurately described) is a very unusual one for the species, and because nobody else has found the plant in the Clova mountains, which are well explored botanically (Corstorphine): Mr E. C. Wallace has searched specifically for *J. macer* there without success. The plant was not again met with in Angus till 1917 (Corstorphine), and in recent years it has not been found there at a greater altitude than 800 ft. (244 m.) (Glen Esk, Corstorphine). Moreover, it may be added that there is a specimen stated to be from Don's garden in Herb. Hooker at Kew.

Scully (1889) and Praeger (1934) both uphold the claim of *J. macer* to be native in south-west, though not in northern, Ireland, on the grounds that it occurs there in very remote, little visited districts, and that it is found in natural habitats, e.g. the salt-marsh on Inishmore, and is not entirely a roadside plant.

There is thus a possibility, though it seems a faint one, that when *J. macer* was introduced into England it was already present as a native in Ireland and, still more doubtfully, in Scotland. Possibly the native and introduced forms were different varieties, only the latter having the capacity for rapid spread. A somewhat similar history has been postulated for some other British plants, e.g. *Crepis taraxacifolia* (Gilmour).

On the continent (cf. Ascherson & Graebner, 1904) its history has been similar to that in Britain, but there is no suggestion that it is anywhere native. It was first observed in the Province of Antwerp, Belgium, in 1824, and in the Province of Utrecht, Holland, in 1825. In Germany it was found in Bavarian Swabia in 1834. During the last century it spread rapidly: by 1906 it was already scattered over almost the whole of Germany and was abundant especially in the north-west German plain and in Oberlausitz. Its present wide distribution in Europe has already been indicated. Graebner (1934) says that though it is absent here and there from wide stretches of Germany, it is yearly advancing farther and the time is not far distant when it will be one of the commonest German plants.

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* The record for East Inverness (96) given by Salmon (1910), and repeated by later authorities, is an error, the note by Traill (*Ann. Scot. Nat. Hist.* 1907, p. 251) quoted by Salmon referring to *J. balticus*, not to *J. macer*.

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L.C. (Ed. 11) No. **1893**

Juncus filiformis L.

By P. W. Richards

Sect. Genuini. A slender wiry perennial, forming not very extensive tufts. Rhizomes slender, horizontal, with very short internodes. Stems stiffly erect, deep or bright green, very faintly ridged when fresh, filiform; pith loose in texture, not interrupted. Inflorescence of seven flowers or fewer, subtended by a bract which usually equals or exceeds the stem in length, so that the inflorescence is placed half-way or lower down the apparent stem. Perianth segments greenish to straw-coloured, lanceolate, acute, 2·5–3 mm. Capsule yellowish brown, glossy, almost spherical, very shortly mucronate, not longer than the perianth.

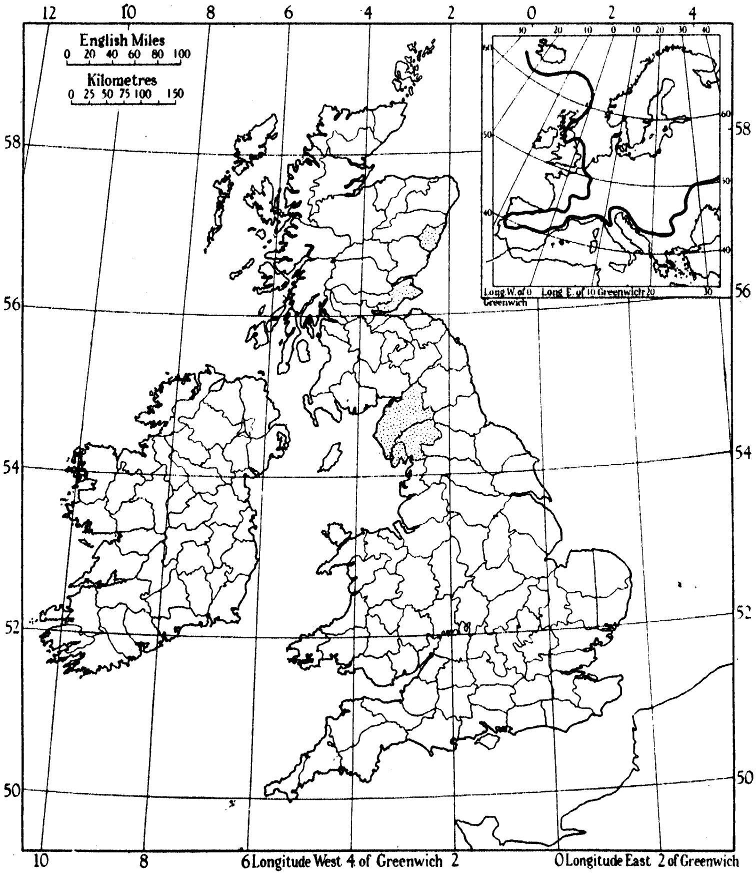

Fig. 1. *J. filiformis* L.: vice-comital distribution in the British Isles and (inset) approximate western and southern limit in Europe.

Shows little variability. In Britain it is as stereotyped ecologically as it is morphologically and is almost confined to a single type of habitat, viz. turf on stony lake shores.

I. *Geographical and altitudinal distribution.* Very local in the British Isles and confined to the English Lake District and a few localities in Scotland. In the Lake District known from Coniston Water and Esthwaite Water in Lake Lancashire (69), Windermere (first found there by Newton in the seventeenth century (Ray, 1688, p. 1305)) and Elterwater (E. C. Wallace) in Westmorland (69) and Lake Lancashire (69), and from Bassenthwaite Lake, Derwentwater, Thirlmere (extinct?), Lowes Water, Buttermere and Crummock Water in Cumberland (70). In Scotland occurs at the Loch of Loirston, Kincardineshire (91), Loch Leven, Kinross (85) and in Dumbartonshire (99). There are doubtful records from Redewater, Northumberland (68) (Rep. B.E.C. 1915, p. 283) and from near St Andrews, Fife (85) (J. H. Wilson, communicated by W. Young).

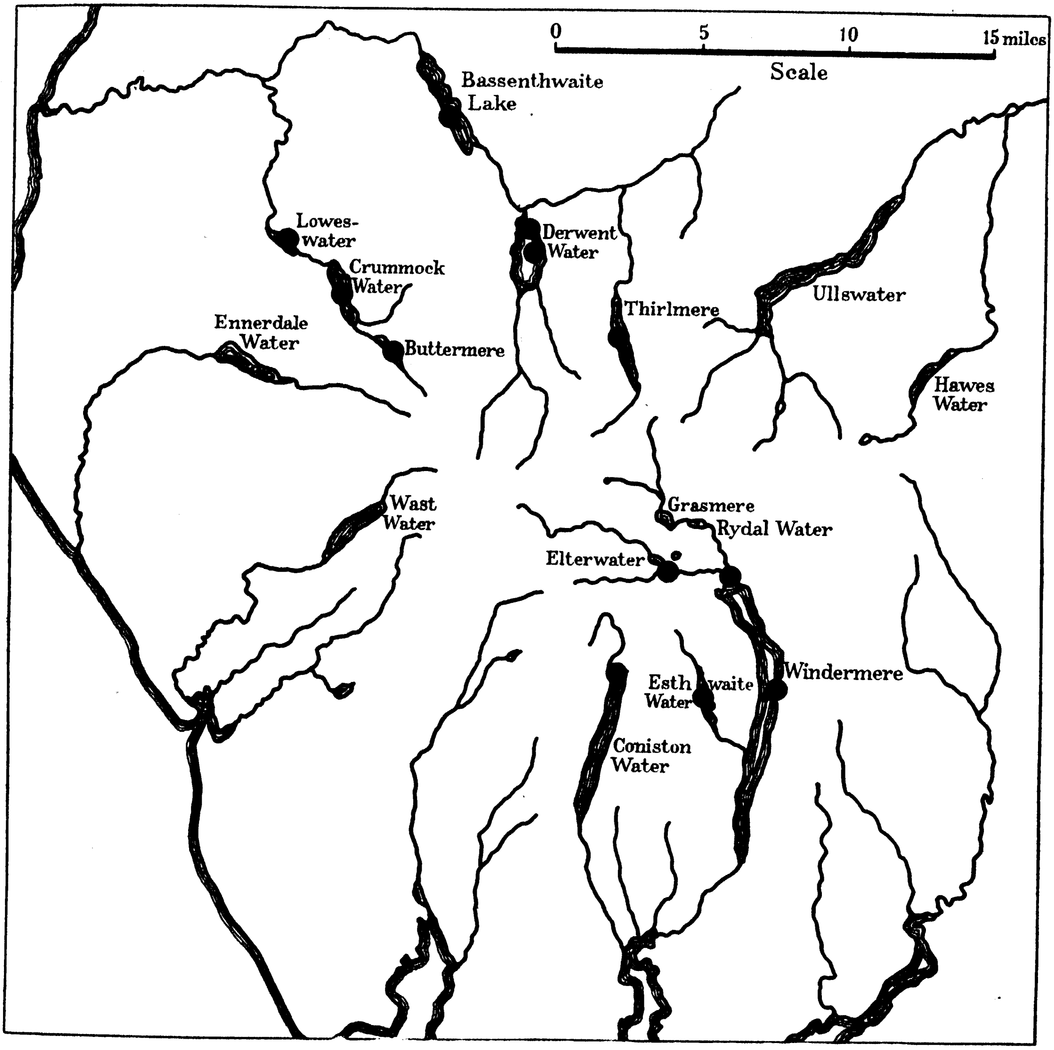

Fig. 2. Sketch-map of the distribution of *J. filiformis* L. in the English Lake District. From published and unpublished records.

Widely distributed in northern and Arctic Eurasia, extending southwards to Belgium, the mountains of Portugal, the Pyrenees, northern Appenines, Balkans and Caucasus, eastwards to Siberia and the Far East. North America from S.W. Greenland and Labrador to British Columbia, south to the mountains of Pennsylvania, Michigan, and in the Rocky Mountains to Utah and Colorado. Patagonia (compare this disjunct distribution with that of *Primula farinosa*).

British localities all lowland, formerly reaching 450 ft. (137 m.) at Thirlmere, but in the Alps it ascends to 2640 m. in Graubünden (Braun-Blanquet & Rübel, 1932, p. 279) and to 2750 m. in Tirol (Kerner, quoted in Ascherson & Graebner, 1904, p. 440), though it is mainly a plant of the subalpine zone (Schroeter, 1926, p. 465).

Tolerant of slight shade (e.g. at Coniston), but usually in unshaded situations.

II. *Habitat.* Almost all the British localities appear to be on stony lake shores: here it grows in open turf formed by *Molinia*, other Junci, etc., usually not on the bare stony or gravelly beach. As the inflorescences are placed so low as to be often overtopped by taller associated plants, it is readily overlooked. At Windermere it grows on an unshaded artificial foreshore built in 1915 (Hay, 1930), but it also grows on a neighbouring natural shore and it has been known at or near the same spot since the seventeenth century; it is found on the very fringe of the turf margin which is in some places slightly undercut by wave action and overhangs the stony shore. The rhizomes are sometimes laid bare by erosion and jut out into the air when the water level is low. On 23 March 1942, when the lake level was 128·66 ft. (39·22 m.) above O.D., *J. filiformis* was at about water level, the rhizomes being submerged and the shoots just emergent. The average summer level (March–September) of Windermere is about 128·5 ft. (39·16 m.) and the winter level (October–February) about 129·5 ft. (39·46 m.) above O.D. Thus in this locality *J. filiformis* grows where it is liable to almost continual submergence in winter and occasional submergence in summer. The soil is alluvial and derived from various hard igneous and old sedimentary rocks: it is very rich in humus, but scarcely peaty. The *p*H is about 6·4 (colorimetric). At Coniston Water it grows below the highest winter drift line in a habitat which is very similar, except that it is slightly shaded by *Alnus*.

The Loch of Loirston, Kincardineshire, is a lake with a very stony shore, the underlying rock being gneiss. "The plant is essentially a member of the fringing flora of the lake, confined to a zone seldom more than 5 or 6 ft. (1·5–1·8 m.) in width. A few isolated plants extend into the open water to a depth of about 4 in. (10 cm.) (Sept. 24, 1941), rooted in the sandy bottom with many stones present." The soil is sandy, its *p*H being about 6·7 (colorimetric) (J. R. Matthews).

As far as is known the British habitats are similar to those at Windermere, Coniston and the Loch of Loirston, with one exception. This is a small area in the North Fen, Esthwaite, where *J. filiformis* occurs on peat (depth unknown) in a fairly luxuriant community including *J. acutiflorus*, *Molinia*, *Carex stellulata* and *C. panicea* as abundant species, and *Hydrocotyle*, *Achillea ptarmica*, and local *Myrica gale* as frequent species. The history of this area is not known, but in position it might represent a development from an old shore line community. The soil *p*H is 4·8 (electrometric) in contrast to that of the gravel swards, usually between *p*H 5·5 and 7·0 (W. H. Pearsall).

The uniformity of habitat in Britain is in striking contrast to the wide range of habitat on the continent, indeed Graebner (1934, p. 129) emphasizes this wide range as a point of special interest. In Germany it occurs especially in dry fertile meadows, less often in wet meadows. It is locally dominant over large or small areas, and there are often large stands especially on alluvial soil near rivers. It also occurs in a very different type of habitat on wet heaths, often with *Erica tetralix* and other damp-loving heath plants, and, like *Juncus balticus*, in dune slacks. In the Alps it occurs in meadows and on moors as well as on screes (Graebner, 1934, p. 129), lake shores (‘*Verlandungsvegetation*’) and in *Schneetälchen* (late snow valleys) (Schroeter, 1926, pp. 465, 645, 838). In the Forez mountains (Central Plateau of France) it is very abundant and locally dominant in bogs by streams at 1350–1400 m., associated with *Sphagnum*, and in Iceland it occurs on the margin of ponds (E. W. Jones).

Its very different ecological behaviour in Britain and on the continent suggests that here it may be represented by only a single ecotype, possibly owing to loss of genotypes during past climatic changes, while on the continent the species may be richer in genotypes and represented by several ecotypes.

III. *Communities.* Occurs at the head of Windermere in a marsh community with the following composition (listed by T. G. Tutin):

Achillaea ptarmica
Agrostis stolonifera
Anthoxanthum odoratum
Aster sp. (introduced)
Caltha sp., cf. radicans
Carex flacca
C. goodenowii
C. ovalis
C. vesicaria
Deschampsia caespitosa
Eleocharis sp.
Festuca pratensis
Filipendula ulmaria
Galium uliginosum
Leontodon autumnalis
Lythrum salicaria
Phalaris arundinacea
Poa pratensis
Polygonum amphibium
Ranunculus acris
Rumex acetosa
Scutellaria galericulata
Trifolium repens
Equisetum arvense
E. limosum
Climacium dendroides

At Coniston the list of species is very similar. At the Loch of Loirston it is a member of the following fringing community (listed by J. R. Matthews):

Agrostis stolonifera var. palustris	a.	Myosotis caespitosa	f.
Carex goodenowii	a.	Potentilla palustris	o.
Galium palustre	a.	Ranunculus flammula	a.
Hydrocotyle vulgaris	f.	R. repens	o.
Juncus articulatus	d.	Veronica scutellata	o.–f.
J. effusus	l.a.	Viola palustris	o.
J. filiformis	(rather sparsely)		

Isolated submerged plants are associated with *Littorella uniflora* (forming a fairly thick carpet), *Eleocharis palustris*, some submerged *Ranunculus flammula* and *Fontinalis antipyretica.*

In the Alps it is found especially in *Caricetum goodenowii* and characterizes a special facies of it on the shores of subalpine and alpine lakes and pools (Braun-Blanquet & Rübel, 1932, p. 279; Schroeter, 1926, p. 443).

IV. Probably subject to and tolerant of moderate grazing, but no definite information.

V. (*a*) *Gregariousness.* Social, occurring (in Britain) in small pure patches, mostly less than 3 dm. in diameter. On the continent it evidently often forms very much more extensive stands (see above, under II).

(*b*) *Performance.* In the Loch of Loirston it is more robust and flowers better in the fringing zone than in the open water (J. R. Matthews).

(*c*) *Effect of frost, drought, etc.* No information.

VI. (*a*), (*b*) *Morphology.* Tufted, but less densely than *Juncus effusus*, from a compact mat of sympodial rhizomes which are horizontal or ascend obliquely when the plant becomes buried by new accumulations of soil (Raunkiaer, 1895–9, p. 390). Much like a miniature of *J. effusus*, and similar in construction, but smaller in all its dimensions. According to Raunkiaer (1895–9, p. 389), in morphology and anatomy, it is nearest among the related species to *J. balticus.* Rhizome slightly below surface of ground or quite superficial, very variable in length; in British specimens the internodes are generally very short, so that the aerial stems are almost touching at the base, but on damp sand they may reach a length of as much as 6 mm.–1·5 cm. (Graebner, 1934, p. 129). The rhizome is slender and bears brown scale leaves; there are numerous spur-branches at the base of the erect shoots. Continuation bud in axil of second scale leaf, flowering shoot in axil of third scale leaf of bud. Flowering shoot bearing up to seven brown sheathing scale leaves, the uppermost of which often bears a short green lamina. Root system adventitious from rhizome, markedly dimorphic, consisting of little branched descending roots and much branched roots growing at the soil surface. Both types of roots have persistent root hairs.

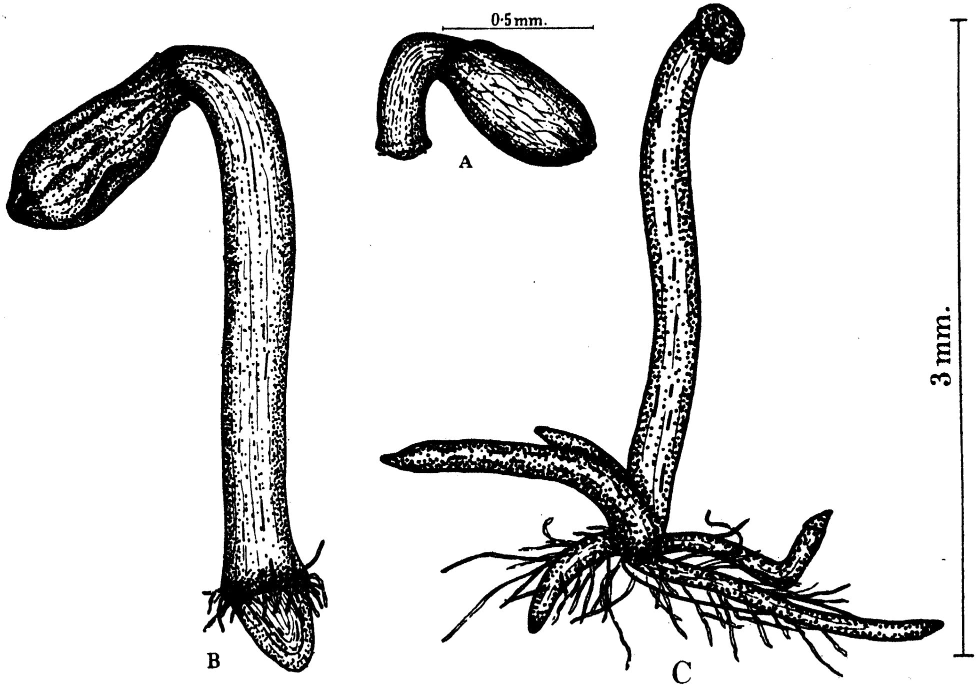

Fig. 3. Three stages in germination of *Juncus filiformis.* Seeds from Windermere, sown in laboratory. A, ×40; B, ×40; C, ×28.

(*c*) *Mycorrhiza.* No information.

(*d*) *Perennation.* Helophyte or semirosette hemicryptophyte, with or without running branches. During the winter only the rhizome remains alive and this is generally submerged from about October to March. Renewal buds at base of erect shoots and at tip of rhizome, thus mostly submerged and buried in soil or superficial.

(*e*) *Vegetative reproduction.* By its mode of growth (see (*b*)), the rhizome forms an effective means of vegetative reproduction.

(*f*) *Longevity.* No information.

(*g*) *Age at first flowering.* No information.

(*h*) *Frequency of seed production.* Every year as far as known.

(*i*) *Ecotypes.* See under II.

VII. *Phenology.* (*a*) No information.

(*b*) New erect shoots appear in March. Numerous slender non-flowering shoots are produced at the end of August–September (T. G. Tutin).

(*c*) In the Lake District it begins to flower in early June (in full flower at Coniston, 7 June 1942, T. G. Tutin) and the fruit is already formed, sometimes ripe, by the beginning of July. Herbarium specimens from the Loch of Loirston show flowers as late as September. In cultivation at Cambridge it came into flower on 14 May 1942. Like most Junci, said to flower in pulses, but, according to Graebner (1934, p. 131), the pulses are less marked than in *J. effusus* and *J. balticus*. The purple-red stigma is visible inside the tip of the flower the day before it opens. The perianth opens about 5 a.m. The anthers dehisce some 1–1½ hours later. The flower is fully developed about 9 a.m. and closes about midday (Graebner, 1934).

(*d*) The seed ripens from July to September or later.

(*e*) No information.

VIII. (*a*) Wind-pollinated, slightly protogynous, but can be self-pollinated (see VII (*c*), above).

(*b*) *Pollinating insects.* No records of insect visitors.

(*c*) *Cleistogamy.* Not observed.

(*d*) *Apomixis.* Probably amphimictic.

(*e*) *Vivipary.* Not observed.

(*f*) *Hybrids.* A hybrid with *J. balticus* is not uncommon on the coast of Germany, etc., but in Britain it does not appear ever to grow in company with that species.

(*g*) *Amount of seed.* Number of seeds per capsule 73–165, mean 124 (nine capsules from Windermere).

(*h*) Seeds dispersed by wind, possibly to some extent by water also. The seeds are covered with a layer of mucilage which swells and causes them to stick together when moistened. Heintze (1915, p. 279) says that in Sweden *J. filiformis* is eaten by cows and reindeer which disperse the seeds in their excretions.

(*i*) *Viability.* Seeds stored under dry conditions are viable for at least 2 years.

(*j*) *Conditions for germination.* Germinates only in the light when grown on moist filter-paper under laboratory conditions.

(*k*) *Morphology of seedlings.* See Fig. 3. The seedlings are very similar to those of *J. effusus.*

(*l*) *Effective reproduction.* No information. Vegetative reproduction doubtless generally effective, but reproduction by seed may also be effective under some conditions.

IX. *Parasites, diseases.* None recorded.

X. *History.* No information. See remarks under II.

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L.C. (Ed. 11) Nos. **367–368**

RHAMNACEAE

Rhamnus cathartica L., **Frangula alnus** Miller (*Rhamnus Frangula* L.)

(The genus *RHAMNUS* sensu lato, L.)

H. Godwin

The two British species of buckthorn were until recently referred to the same genus. They are here separated into the genera *Rhamnus* L. and *Frangula* Miller, a separation held by some taxonomists to be unreasonable. The genus *Rhamnus* in the wide sense consists of shrubs or trees with simple alternate or opposite leaves, and small cymose clusters of flowers which are small, sometimes unisexual, and green or yellow in colour. The urceolate calyx tube is adnate to the base of the ovary and its inner surface forms a nectary. The drupaceous fruit encloses 2–4 'stones' (pyrenes). The genus *Rhamnus* in this wide sense is divisible into two sections:

1. *EU-RHAMNUS*. Flowers usually four-merous, polygamous or dioecious; style cleft, buds with bud scales. Cotyledons epigeal. (Including *Rhamnus cathartica* L., *R. alaternus*, etc.)
2. *FRANGULA*. Flowers usually five-merous, hermaphrodite; style entire, buds naked. Cotyledons hypogeal. Chiefly a North American genus. (Including *Frangula alnus*, *Rhamnus Purshiana*, etc.)

INSECTS, MITES AND FUNGI ASSOCIATED WITH THE TWO BUCKTHORNS

INSECTS AND MITES. (O. W. Richards)

c. = *Rhamnus cathartica*, *f.* = *Frangula alnus*

The following list includes only species closely associated with *Rhamnus* sensu lato, not polyphagous species. They have all been observed in Great Britain, though confirmatory evidence has been obtained from continental literature. Where the name of an insect species is not marked with either *c.* or *f.* the record is for '*Rhamnus*', the species not having been specified. In most of such cases both species of *Rhamnus* are likely to be eaten. The British distribution of the insect is given when this is sufficiently known.

HEMIPTERA-HOMOPTERA

Aphididae: *Aphis rhamni* Boyer, *c.*, *f.*, on tips of shoots, migrating to potato in summer. *A. frangulae* Kalt., *c.*, *f.*, on leaves.

Psyllidae: *Trichochermes walkeri* Först., *c.*, *f.*, leaf margins rolled upwards, much thickened, often red, Kent to Glos. *Trioza rhamni* Schrk., *c.*, small, shallow depressions on lower margin of leaf, Norfolk to Glos. *Psylla rhamnicola* Scott, *c.*, on leaves, Kent to Glos.

Typhlocybidae: *Erythroneura rhamnicola* Horv. (*rhamni* Edw.), *c.*, *f.*, on leaves, Glos.

DIPTERA

Cecidomyidae: *Contarinia rhamni* Rubs., *f.*, larva in the flowers which are closed. Bagnall & Harrison (1921, p. 154) and Bagnall (1931) record what is almost certainly this species as '*Perrisia' rhamni. Dasyneura frangulae* Rubs., *f.*, larva in the flowers which are closed. Bagnall & Harrison (1921, p. 167), and Bagnall (1931) record what is almost certainly this species as '*Contarinia' frangulae. Asphondylia* sp., by locality probably *c.*, larva in swollen fruit, Letchworth (F. W. Edwards) (Barnes in litt.). Cecidomyidae sp., *c.*, *f.*, fruit swollen (cf. Honard, no. 4067). Recorded by Bagnall (1931). Cecidomyidae sp., *c.*, blister gall on leaf with yellow larva (Bagnall, 1931).

LEPIDOPTERA

PIERIDAE: *Gonepteryx rhamni* L., larva common on leaves, England and Ireland.

GEOMETRIDAE: *Philereme vetulata* Schiff. and *P. rhamnata* Schiff., larva rather common on leaves, England.

TORTRICIDAE: *Phtheochroa sodaliana* Haw., *c.*, larva in the berries, England. *Ancylis derasana* Hb., *c.*, larva on leaves, Britain to Clyde, rather local. *A. siculana* Hb., *c.*, *f.*, larva on leaves, Britain to Caledonian Canal, especially eastern. *A. obtusana* Haw., *c.*, *f.*, larva on leaves, England, rather local.

COSMOPTERYGIDAE: *Chrysoclista rhamniella* Zell., larva in shoots, afterwards in rolled leaves, eastern England to Sussex and Westmorland.

LYONETIIDAE: *Bucculatrix frangulella* Göze, *c.*, *f.*, larva mining when young, afterwards externally on leaves, England, rather common.

NEPTICULIDAE: *Nepticula catharticella* Staint., *c.*, larva mining leaf, England to York, local.

ACARINA

ERIOPHYIDAE: *Eriophyes annulatus* Nal., *c.*, leaf hypertrophied underneath between midrib and lateral vein (Bagnall, 1931).

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FUNGI (A. SMITH)

Frangula alnus and *Rhamnus cathartica* appear to be little troubled by parasitic fungi. Common to both is the aecidial stage of the heteroecious rust *Puccinia coronata* Corda, which may be very conspicuous, but is in all probability of but slight biological importance. Various grasses act as alternate hosts. There is a strict biological specialization and the forms are confined to their own aecidial hosts. The form on *Rhamnus cathartica* was separated on biological rather than on morphological grounds as *Puccinia Lolii* by Nielsen, but recently Miss M. R. Brown (1936, 1937, 1938) has reunited them.

Silvering of foliage of *Frangula alnus* has been noted at Wicken Fen and fructifications of *Stereum purpureum* Pers. collected later from the affected tree. Some attention has been given to a dieback of this host at Wicken Fen by Stevenson and then by Baker (1936). The only fungus specifically identified was *Nectria cinnabarina* (Tode ex Fr.) Fr., and this together with a species of *Fusarium* proved parasitic on test. Further work (unpublished) would appear to suggest that a species of *Cytosporina* may be of some importance (F. T. Brooks).

The following is a list of saprophytes recorded on *Frangula alnus* (a few may actually be parasites—the literature is silent on the matter):

ASCOMYCETES

PEZIZALES: *Tympanis frangulae* Fr. recorded also as Dermatella and Scleroderris with *Micropera versiformis* (Sphaeronema) as its conidial stage.

HYPOCREALES: *Nectria punicea* (K. & Schm.) Fr.

SPHAERIALES: *Diaporthe syngenesia* (Fr.) Fuck.; *Cucurbitaria rhamni* Fuck.; *Karstenula rhodostoma* (Fr.) Speg.; *Lophiostoma quadrinucleatum* Karst.; *Bagnisiella rhamni* (Mont. ex Cooke) Berl. & Vogl.

COELOMYCETES: *Phyllosticta rhamni* West; *Diplodia frangulae* Fuck.; *Hendersonia mammiliana* Currey; *Dichromera saubinettii* Cooke.

The following have been recorded on *Rhamnus cathartica*:

DOTHIDEALES: *Systremma frangulae* (Fuck.). Theiss. & Sydow.

SPHAERIALES: *Diaporthe extensa* (Fr.) Sacc.; *Diaporthe fibrosa* (Pers. ex Fr.) Nits. in Fuck.

These two species have been united under the former name by some authors.

COELOMYCETES: *Phyllosticta rhamnicola* Desm. It should be noted that *Trichobasis rhamni* Cooke has no reality—the fungus was, it is thought, plum rust on a plum.

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L.C. (Ed. 11) No. **367**

Rhamnus cathartica L.

H. Godwin

A bush or small tree. Stems spinous, with rather regular branches in pairs almost at right angles to the main stem (hence the German name, *Kreuzdorn*), rough with projecting bases of dead lateral shoots. Bark blaze orange and young wood whitish, old bark fissured and scaling. Dead wood hard and purplish. Buds with dark bud scales. Leaves deciduous, ovate, serrate, with dull green surface, becoming yellow or brownish (not red) before falling; young leaves downy beneath, veins strongly converging. Flowers dioecious, tetramerous, in dense clusters on persistent dwarf shoots. Stigma 4-cleft. Fruits 6–10 mm.

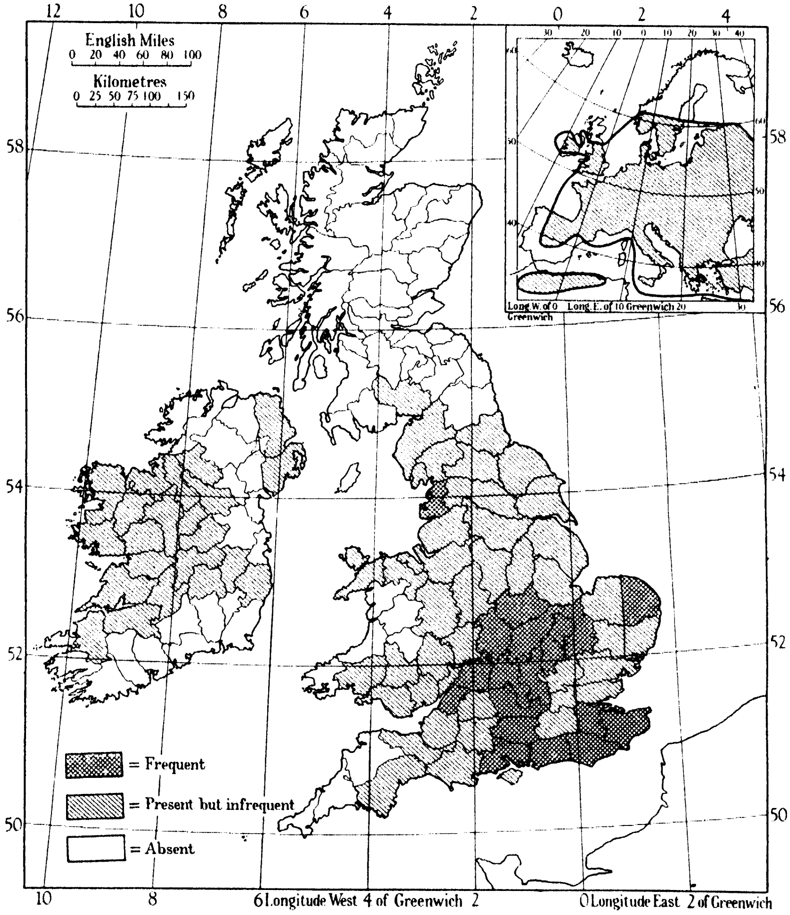

Fig. 1. *Rhamnus cathartica* L., vice-comital distribution in the British Isles, and (inset) European distribution.

across, turning from green to black on ripening, with three or four pyrenes per drupe. Pyrenes obovoid with quadrant or triangular cross-section, and small furrow at base of inner edge. Germination epigeal: cotyledons 2, heart-shaped.

Wood closely diffuse-porous, strongly flecked in transverse section due to mosaic arrangement of vessels and fibres. Perforation in vessels simple, some spiral thickening; very little xylem parenchyma, medullary rays, uniseriate and biseriate, slightly heterogeneous.

Not a very variable species, strongly calcicole and common in seral communities, chiefly scrub on alkaline peat and on limestone soils.

I. *Geographical and altitudinal distribution.* (*a*) Absent in Cornwall, north Devon, Northumberland and five Welsh counties (Pembroke, Cardigan, Radnor, Merioneth, Montgomery), but otherwise present throughout England and Wales. Doubtfully native in Scotland, except possibly in Dumfries. In England particularly frequent in the midland, southern and eastern counties with big outcrops of calcareous rock, especially chalk and oolite, or large alkaline fens. In Ireland present in a wide belt across the central Irish plain, but absent from the southern counties, and absent or rare in the northern.

Possibly warmth and sunshine requirements as well as soil factors limit the species, some indication of this being given by the low altitudinal range and conditions for ripening fruit.

Extending through greater part of Europe to 60° 48′ in Norway and 61° 41′ in Sweden, in southern Finland, Esthonia and across Russia into western Asia, Afghanistan and Turkestan.

In southern Europe to middle and eastern Spain and Macedonia, present sparingly at high altitudes in north Africa (Morocco and Algeria), but absent in the Balearics, Corsica, Sardinia and Greece. Present from western Siberia, Transcaucasia to the Altai: shows a rather marked limitation towards the Atlantic in the British Isles and Iberia. Broadly speaking absent from Scotland, infrequent or absent in Ireland and parts of the west of England and Wales, but abundant in Midlands and south-east England.

(*b*) Lowland, taken by Watson (1847) as 'index plant' for altitudinal zones; '*R.c.* without Clematis' indicates his 'Mid-Agrarian Zone' which in Britain extends up to 900 ft. (274 m.), there being no *R.c.* in the 'Super-Agrarian' zone; to 1100 ft. (335 m.) on Dirtlow Rake, Derbyshire (Linton, 1903).

To 5300 ft. (1600 m.) in Engadine (Graebner, 1933), 5100 ft. (1550 m.) in Mittelbünden, Switzerland (Braun-Blanquet & Rübel, 1932–6), 5100 ft. (1550 m.) in Valais (Hegi), 5900 ft. (1800 m.) in Morocco (Jahandiez & Maire, 1931–4).

(*c*) Avoids dry exposed places on the chalk (J. F. Hope-Simpson), and is intolerant of shade, being found as undershrub only in open woodlands.

II. *Habitat.* Occurs in four chief habitat types in Britain: (1) on alkaline fen peat (e.g. Wicken Fen and Norfolk Broads); (2) in seral scrub on limestone soils, especially the chalk, but also on Jurassic limestones and Carboniferous limestone in Mendips and Pennines; (3) as hedgerow plant very widespread on limestone soils; (4) as undershrub with other calcicolous shrubs in ashwoods or oakwoods on limestone soils.

(1) *Alkaline fen peat* (Wicken Fen). Humified black sedge or wood peat with freshwater shells; water-table at or above soil-level in winter but falling a few decimetres in

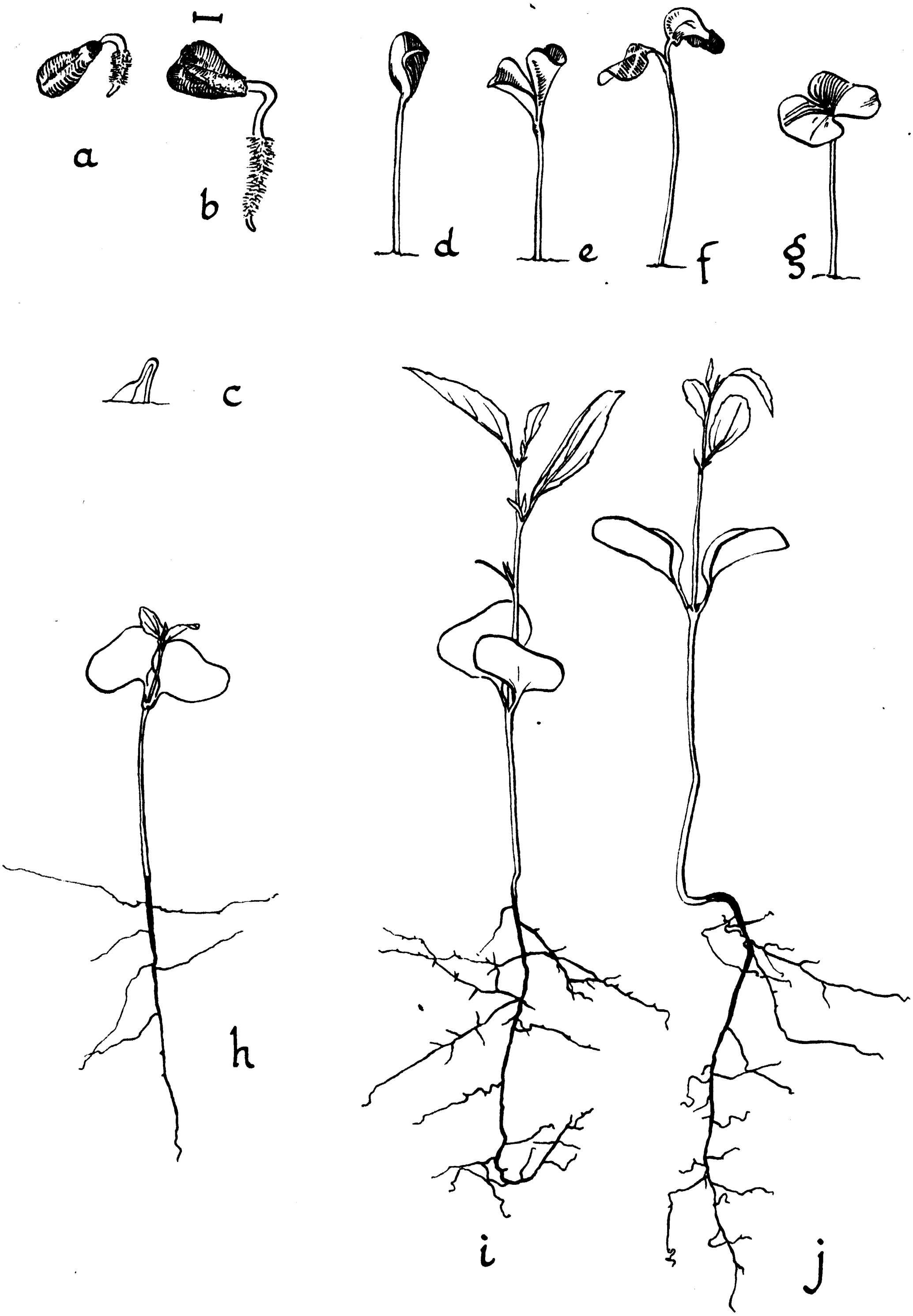

Fig. 2. Stages in germination of *Rhamnus cathartica*, all gathered from Wicken Fen: *a–g*, June; *h–j*, September.

summer (Godwin & Bharucha, 1932); earthworms absent, but more or less replaced by Cladocera (Omer-Cooper, 1925); *p*H 6·5–8·5 (48 colorimetric observations at depths 5–15 cm.); humus content 68·0% at 20 cm.; average $CaCO_3$ content of five samples from upper 20 cm. 0·25% (Bharucha, 1932); mean pore space of top 20 cm. 3·5–20·0% (Bharucha, 1932); oxygen content of soil water practically nil (Bharucha, 1932; Conway, 1936–8), of aerated top soil varying. Carbon dioxide content of soil air high-order of 1–6% at 20 cm. depth with regular seasonal change. Oxygen varying inversely, but not below about 12% at 40 cm. (Conway). Water content of soil always very high, never nearing wilting coefficient. Light intensity beneath old carr of *R. cathartica* 5 m. tall, *c.* 3% of external intensity in July sunshine (Bharucha). Soil temperatures under old carr show greater variability than under thick herbaceous vegetation (Godwin, Mobbs & Bharucha, 1932).

(2) *Calcicolous scrub*, especially on the chalk. Mostly shallow rendzina soils with alkaline reaction (*p*H 7–8), and high carbonate content. Exact data in relation to *R. cathartica* lacking, but results to be expected of this order: soil depth 18–76 cm.; $CaCO_3$ in top 15 cm. 33–60%; loss on ignition in top 15 cm. 13–23%; *p*H in top 15 cm. 7·6–7·9 (juniper and hawthorn seres on Chalk in Chilterns (Watt, 1934)). Absent from scrub of chalk heaths, surface *p*H 6·5–7·0 (J. F. Hope Simpson).

In scrub on mountain limestone in Derbyshire and Mendips, but avoiding wind exposure more in the former locality (T. G. Tutin). Characteristic of scrub on the limestones of the central plain and west of Ireland (Praeger, 1934): also on the Silurian in Ireland. Occasionally local in scrub on modified heath soils, e.g. South Haven Peninsula, Dorset, where formerly cultivated (C. Diver).

(3)–(4) In hedgerows and woodlands showing similar soil preferences to scrub. In English midlands on all geological formations from Lower Lias to present day (Horwood & Noel, 1933), but strong preference for calcareous soils.

Europe. On all types of soil (Braun-Blanquet & Rübel, 1932–6), but most frequent and most flourishing on limestone soils. 'Gern auf Kalk, doch bisweilen auch völlig bodenvag' (Hegi, 1935). On base-rich peat soils possibly less common than in Britain.

III. *Communities.* (1) *On alkaline peat.* Characteristic of seral communities. At Wicken Fen, Cambs, colonizes Cladietum and Cladio-molinietum if left uncut, together with *Frangula alnus, Salix atrocinerea, Viburnum opulus, Crataegus monogyna.* In the early seral stages less frequent than *Frangula,* but tending to replace old Franguletum by almost pure Rhamnetum catharticae, and rapidly excluding *Salix atrocinerea.* Within Rhamnetum:

Agrostis stolonifera var. palustris	v.a. (locally)	Lysimachia vulgaris	f. (not flowering and relict)
Rubus caesius	v.a.	Symphytum officinale	f. (not flowering and relict)
Thelypteris palustris	v.a.	Urtica dioica	f.
Convolvulus sepium	a. (not flowering in relict)	Hypnum cuspidatum	a.
Iris pseudacorus	a.	Mnium affine	f.

In early stages of colonization a diffuse many-stemmed bush, but in old Rhamnetum forming a single-stemmed tree with dense crown. Young bushes very shade tolerant. In carr of *Alnus-Salix atrocinerea* in fens of the Little Ouse and Waveney valleys as scattered bushes, with undergrowth of *Calamagrostis lanceolata, Cardamine pratensis, Carex acutiformis, C. elata, Dryopteris dilatata, Filipendula ulmaria, Iris pseudacorus,* *Lycopus europaeus, Mentha aquatica.* As scattered bushes, together with *Frangula alnus*, in *Alnus-Betula pubescens-Salix atrocinerea* carr of Norfolk Broads (Pallis, 1911):

Alnus glutinosa	a.	Quercus robur	o.
Betula pubescens	a.	Rhamnus cathartica	a.
Frangula alnus	a.	Ribes nigrum	o.
Fraxinus excelsior	f.	Salix atrocinerea	a.
Ligustrum vulgare	o.	Viburnum opulus	a.

with fen undergrowth of type indicated above.

(2) *In calcicolous scrub.* A characteristic component of chalk scrub along with the shrubs, *Clematis vitalba, Cornus sanguinea, Crataegus monogyna, Euonymous europea, Juniperus communis, Ligustrum vulgare, Prunus spinosa, Sambucus nigra, Viburnum lantana,* and trees such as *Fagus silvatica, Fraxinus excelsior, Quercus robur, Sorbus aria, S. aucuparia, Taxus baccata.* The undergrowth, very variable in density, is either relict from colonized grassland or represents early invasion of a woodland flora. In the Chilterns has highest constancy grade in scrub of both hawthorn and Juniper seres, together with *Cornus sanguinea, Crataegus monogyna, Fagus silvatica, Ligustrum vulgare, Prunus spinosa, Rosa canina, Rubus fruticosus* (agg.), *Sorbus aria,* and *Viburnum lantana.* Does not persist into the beech consociation (Watt, 1934).

On western Irish limestone crags in dense *Corylus* scrub with *Cornus sanguinea, Euonymus europaeus* and *Frangula alnus.* On the Burren in scrub with *Corylus, Crataegus, Euonymus, Fraxinus, Ilex, Prunus spinosa,* some *Cornus* and *Frangula alnus.* Also in the rich crevice vegetation of the limestone pavements of the Burren and on the Aran Islands (Praeger, 1934).

(3) *Hedgerows.* Species lists like those of calcicolous scrub. *Rhamnus cathartica* may be more abundant in hedges at foot of chalk escarpments than in scrub on scarp itself (A. R. Clapham).

(4) *Woodland underscrub.* Occurs with other calcicolous shrubs in English ashwoods on limestone especially in Pennines and Somerset, in openings and margins of Quercetum roburis (Lake District) (T. G. Tutin). In old ash-oak wood on Cotswold Oolite in Guiting Wood, Glos., where standards are removed or in bad condition; here calcicole shrubs include *Acer campestre, Cornus sanguinea, Euonymus europaeus, Sorbus aria, Viburnum lantana, V. opulus*; chief ground dominants *Mercurialis* and *Scilla,* but also *Colchicum autumnale, Convallaria majalis, Habenaria chlorantha, Helleborus viridis, Lathraea squamaria, Orchis mascula, Paris quadrifolia* (A. R. Clapham).

In marginal scrub and as a woodland scrub throughout open woodlands on base-rich soils. In Ireland with *Frangula alnus* in relicts of natural woodland on limestone, e.g. Clonad Wood near Tullamore, in Killarney, both species favouring limestone rather than Old Red Sandstone soils. On Ross Island (Killarney) with *Arbutus Unedo* (Praeger, 1934).

Europe. Widespread but local in sunny, stony and dry places, in scrub, woodland, hedges, with preference for south and west slopes, or on wet soils in fenwoods. In mixed woods of conifers and deciduous trees, and on lighter soils as undergrowth in pinewoods. In north Africa restricted to high altitudes.

IV. *Response to biotic factors.* Colonization is suppressed by sedge- and litter-cropping at Wicken Fen, but rapidly follows removal of the deflecting factor. Regenerates strongly from cut stools, and after grazing and burning: common as planted hedgerow shrub in

U.S.A., resistant to cattle-grazing, cannot resist heavy rabbit attack on the Chalk (J. Hope-Simpson), rabbits damage bark (C. Elton).

V. (*a*) *Gregariousness.* Moderately gregarious, depending on density of seed disposal. Very strongly associated with hedgerows—possibly a bird-dispersal effect.

(*b*) *Performance in various habitats.* Commonly as a many-stemmed bush up to 10 or 15 ft. (3–5 m.) tall, but when older forming a small tree (e.g. Wicken Lode bank): height 31 ft. (9·4 m.), crown diameter 22 ft. (6·7 m.) and girth at 4 ft. from ground 2·1 ft. (0·6 m.). On the Chalk sometimes showing chlorosis.

(*c*) *Effect of frost, drought, etc.* Seedlings on peat soils suffer heavily from frost.

VI. *Morphology, etc.* (*b*) On alkaline peat the whole root system is in the top few centimetres of soil above the water-table.

(*c*) *Mycorrhiza.* The whole root system both in seedling and mature plant is mycorrhizal. In effect, all young functional roots are mycorrhizas. The association is endotrophic with a member of the arbuscular-vesicular group of fungi. The mycelium is mainly intracellular in distribution, affecting especially the inner zone of cortical tissues. Large pear-shaped vesicles are formed in this material (coll. Wicken Fen—October), and the intracellular complexes undergo digestion giving rise to a characteristic sporangiole stage (M. C. Rayner).

(*d*) *Perennation.* Deciduous microphanerophyte with bud scales on winter buds.

(*e*) *Vegetative reproduction.* Unrecorded.

(*f*) *Longevity.* Not recorded.

(*g*) *Age at first flowering.* Flowers and fruits very early, certainly at 11 years.

(*h*) *Frequency of seed production.* Seed is set freely every year in southern Britain.

(*i*) *Ecotypes.* Unreported.

(*j*) *Chromosomes.* Not recorded.

VII. *Phenology.* (*a*) Time of maximum root growth not known.

(*b*) Leaves appear about late April, early May (Wicken, 1934, 1935, V. M. Conway; Hants, 1938, C. Elton).

(*c*) Leaves fall, October, November; flowering May–June; June (Wicken, 1934, V. M. Conway; Hants, 1938, C. Elton). Average date of first flowering in Wilts, 4 June (Preston, 1888). Flowering season restricted, no flowers being left as green fruits become black.

(*d*) Fruits mature during September (Wicken, 1934, V. M. Conway) and October, but show a strong tendency to remain on the branches, some remaining after December.

(*e*) On fen peat germination takes place throughout spring and summer.

VIII. (*a*) *Mode of pollination.* The species is dioecious as reported by Darwin (1877). Petals and sepals are shorter and narrower in the female flowers than in the male, and sepals in female flowers do not turn down at maturity. Vestigial stamens are present in the female flowers, which are reported to show dimorphic heterostyly.

In male flowers the stigmas are of very variable length at the time of staminal dehiscence, from about 0·8 to 0·2 of the length of the receptacle cup. At staminal dehiscence the anthers almost meet above the cup-like receptacle leaving a small central passage between the introrse anthers.

Counts of old bushes in fruit at Wicken Fen and Gog-Magog Hills showed a ratio of 6 : 1 or 7 : 1 of fruiting to non-fruiting bushes; later examination confirmed that this was the ratio of female to male bushes. Statistical analysis indicated that there is no change in the ratio with age or habitat condition at Wicken (D. G. Catcheside).

Near Leatherhead I. H. Burkill in a count of 61 bushes reports a small excess of fruiting over non-fruiting bushes. The yellowish green flowers are strongly honey-scented and clearly insect-pollinated. The urn-shaped calyx tube has nectarial lining.

(*b*) *Insect visitors*. Abundant but little recorded. Records for Germany include *Eristalis nemorum* L. (Kiel), and *Bombus hypnorum* L. (Styria) (Knuth, 1906–9).

British records: Apidae—*Andrena synadelpha* Perk. (Coulsdon, Surrey, 6 June 1937); Diptera, Stratiomyidae, *Pachygaster atra* Pz. (Goring, Oxon, 10 July 1934) (O. W. Richards).

(*c*) *Cleistogamy*. Improbable.

(*d*) *Apomixis*. Presumably amphimictic.

(*e*) *Vivipary*. Not recorded.

(*f*) *Hybrids*. No hybrids known.

(*g*) *Amount of seed*. Usually three pyrenes per fruit, sometimes four. Female bushes fruit heavily, e.g. a many-stemmed bush, 7 ft. (2·1 m.) tall, bore 1455 fruits on 27 September 1932 (Godwin, 1936). Kinzel (1926) reports that in exposed places few fruits are produced and many of these have non-viable seeds.

(*h*) *Dispersal*. Fruits presumably taken by birds, but Woodruffe-Peacock (1918) says: ‘it is not beloved of birds except when the hunger of long-continued rough weather perforce drives them to its berries...it is always alimentary-canal carried, and never taken till all other hedge-fruit is gone.’ Late retention of fruit on bushes strengthens the above impression; the early shedding of the fruit in *Frangula alnus* is liable to suggest that its fruit is more palatable to birds.

German records (Schuster, 1930): field-fare (*Turdus pilaris*), missle-thrush (*T. viscivorus*), red-wing (*T. musicus*), song-thrush (*T. ericetorum*), blackbird (*T. merula*), robin (*Erithacus ruberula*), wax-wing (*Bombycilla garrulus*), great-tit (*Parus major*), bullfinch (*Pyrrhula pyrrhula*).

British records: pheasant (*Phasianus colchicus*), ring-dove (*Columba palumbus*), jay (*Garrulus glandarius*), blackbird (*Turdus merula*) (Lincs) (Woodruffe-Peacock, 1918), marsh-tit (*Parus palustris*) (Oxford) (W. B. Alexander). Burkill & Willis (1893) report *Rhamnus cathartica* growing in tops of pollard willows near Cambridge, doubtless bird carried.

Praeger (1913) reports dry fruits float 6 days and pyrenes 3½ days.

At Wicken Fen when fruits fallen to ground dry and expose pyrenes these are taken by mice, and planted stones are apparently also taken, but there is no evidence of mouse dispersal. Extracted pyrenes were also slowly removed from a tray out of reach of mice, presumably by birds (Godwin, 1936).

(*i*) *Viability*. Not known: at least 2 years.

(*j*) *Conditions for germination*. Stones expressed from fruits in September when first ripe give 90–100% germination, but this falls off if the extracted stones are allowed to dry. It can sometimes be restarted by cutting the endocarp. In Cambridge seeds gathered in September and sown in November show about 50% germination at laboratory temperatures, the remaining 50% held in same conditions germinate in following spring.

Kinzel (1926) reports that conditions of exposure during ripening affect the germination: seeds from plants grown in exposed places are more sensitive to frost than those from milder places. According to Kinzel seeds germinate equally well in darkness or light (confirmed by author) and are somewhat susceptible to frost; sown in autumn they show a high percentage germination in following spring.

(*k*) *Morphology of seedlings.* Germination is epigeal, and the two cotyledons large, thin and cordate. They remain attached and green on the seedling for some months (see Fig. 2).

(*l*) *Effective reproduction.* Entirely by seed.

IX. *Parasites: diseases.* See composite lists for two buckthorns on p. 67.

X. *History.* Wood and fruits identified by Clifford in wood peat at Peacocks Farm, Shippea Hill, Cambs, just above Neolithic 'A' horizon, in Pollen-Zone VII (of Godwin) (Clark, Godwin & Clifford, 1935). Stem and fruits also found by Clifford at Woodwalton Fen, Hunts, in wood peat at a level corresponding to maximum extension of fen clay, below this, as well as just above and just below this clay, i.e. late Neolithic to Bronze Age (Godwin & Clifford, 1938). Charcoal of Neolithic age from Anglesey (Phillips, 1935).

L.C. (Ed. 11) No. **368**

Frangula alnus Miller (*Rhamnus frangula* L.)

H. Godwin

Bush or small tree, stems unarmed, branches not very regular, in alternate pairs at much less than a right angle to main stem. Bark on young shoots green, becoming grey-brown. Bark blaze lemon-yellow, young wood dark brown. The old bark smooth except in very old trees and peeling readily off dead wood, which is soft and has no purplish colour.

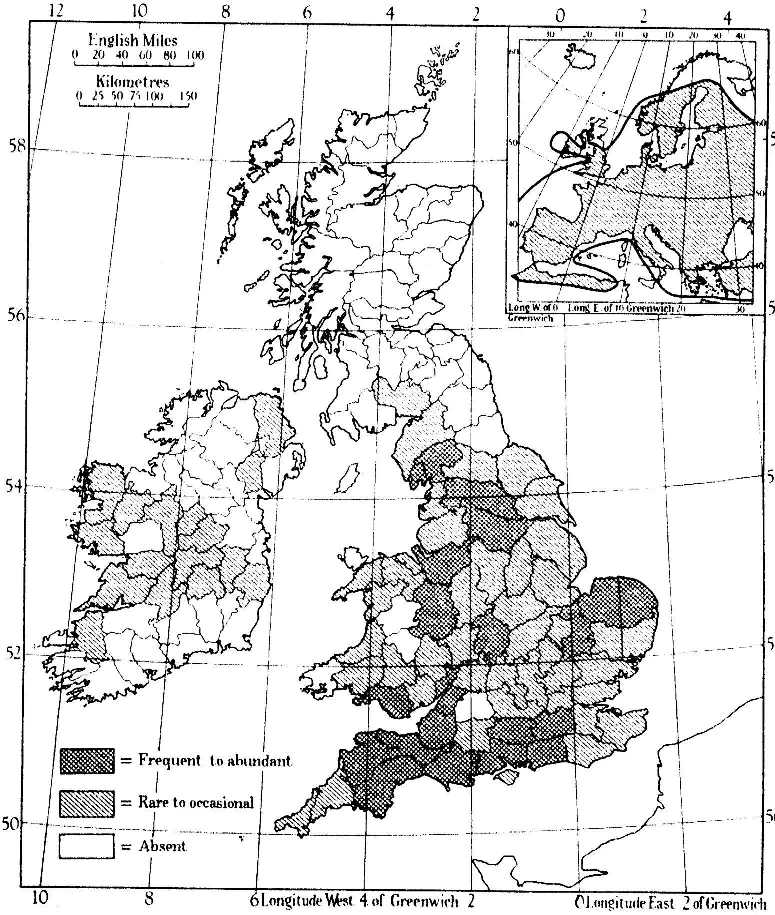

Fig. 1. *Frangula alnus* Miller, vice-comital distribution in the British Isles, and (inset) European distribution.

Buds naked, consisting of miniature leaves heavily clothed in brown hairs. Leaves obovate, produced to a more or less pointed tip, margin entire but wavy, with signs of serration only in seedlings. Upper surface shining, veins markedly parallel. Leaves becoming clear yellow and red in autumn. Flowers pentamerous, bisexual, borne in small groups in the leaf axils on first year shoots. Stigma entire. Fruits 6–10 mm. across, changing from green to red, and then to violet-black on ripening: from mid-season buds, flowers and fruits of all stages of ripening present together. Usually two (sometimes three) pyrenes in each drupe. Pyrenes compressed, broadly obovoid, about 5 mm. long and 2 mm. thick, with faint ridge down inner face and deep furrow at base formed of two humps of the testa projecting through the endocarp. Germination hypogeal. Wood weakly ring-porous, vessels slightly radial with spiral thickening and simple perforation: some scattered xylem parenchyma. Uniseriate and narrow medullary rays (× 3): slightly heterogeneous.

Not a very variable species. The narrow-leaved 'var. *angustifolia*' known in cultivation, was once found in Wicken Fen, Cambs, but its seeds yielded normal plants. Strongly seral in habitat preferences, avoiding all but light shade: on a wide range of soil types though usually with considerable ground moisture.

I. *Geographical and altitudinal distribution.* Broadly speaking, absent from Scotland, infrequent in Ireland, rather widespread and locally very common in England and Wales. Absent from four Welsh counties (Pembroke, Radnor, Montgomery and Anglesey) and from north Wilts, Durham, Northumberland and the Isle of Man, also distinctly rare in the following central English counties: Hereford, Oxford, Northants, most of Bucks, Herts, most of Berks, Middlesex, south Wilts. This may be due in part to the geological structure and scarcity of moist uncultivated soils: correspondingly the high frequencies in other counties (see map) are related to frequency of such conditions. Possibly warmth and sunshine requirements as well as soil factors limit the species, as indicated by its low altitudinal range. There is indication of considerable diminution of frequency in the Isle of Wight during the last 100 years, possibly as a result of modifications in woodland management. Extending through greater part of Europe to 64° 30′ in Norway, 65° 30′ in Sweden, 64° 30′ in Finland and 66° 50′ in Russian Lapland: in Russia to north tip of Lake Onega through Wologda and Perm to Urals and Siberia. In southern Europe through almost full length of Portugal and Spain: in France rare towards Mediterranean: just entering north Africa in Algeria and Morocco: all Italy, Thessaly, Corfu, and Turkey to Asia Minor and Transcaucasia, but absent from Sicily, Corsica and the Balearics.

Given by Watson (1847) as a lowland species throughout Britain, i.e. below 1000 ft. (305 m.), to 4600 ft. (1400 m.) in Valais and Tirol, 4650 ft. (1420 m.) in Graubünden (Braun-Blanquet & Rübel, 1932–6), 4900 ft (1500 m.) in Churfirsten.

In Britain avoiding heavy shade, but apparently in central and southern Europe more characteristically a woodland species.

II. *Habitat.* Occurs in the following habitats in Britain: (1) in seral scrub on alkaline fen peat (e.g. Wicken Fen, Norfolk Broads); (2) as scattered scrub on margins or modified surfaces of raised bogs (Lancs and Cheshire 'mosses', Somerset 'Heaths'); (3) as scrub on usually moist heaths and commons on a wide range of geological formations (e.g. Barton Clay, Headon Beds, Bagshot Beds, Reading Beds, London Clay, Weald Clay, Lower Greensand, Bunter Sandstone, and the Culm); (4) marginal scrub of valley bogs (Hants) and near seepage lines at junction of sands and gravels with less permeable rocks; (5) in limestone scrub, often Coryletum (e.g. west Ireland and Lake District); (6) as scattered undergrowth in woodland developed in all the above habitats (e.g. in Alneto-Betuletum in Broads and at edges of Lancs raised bogs, in pine plantations in the home counties, in oak-hornbeam woods in Herts, beechwoods at Burnham beeches, *Quercus sessiliflora* woods on limestone soils in Ireland.

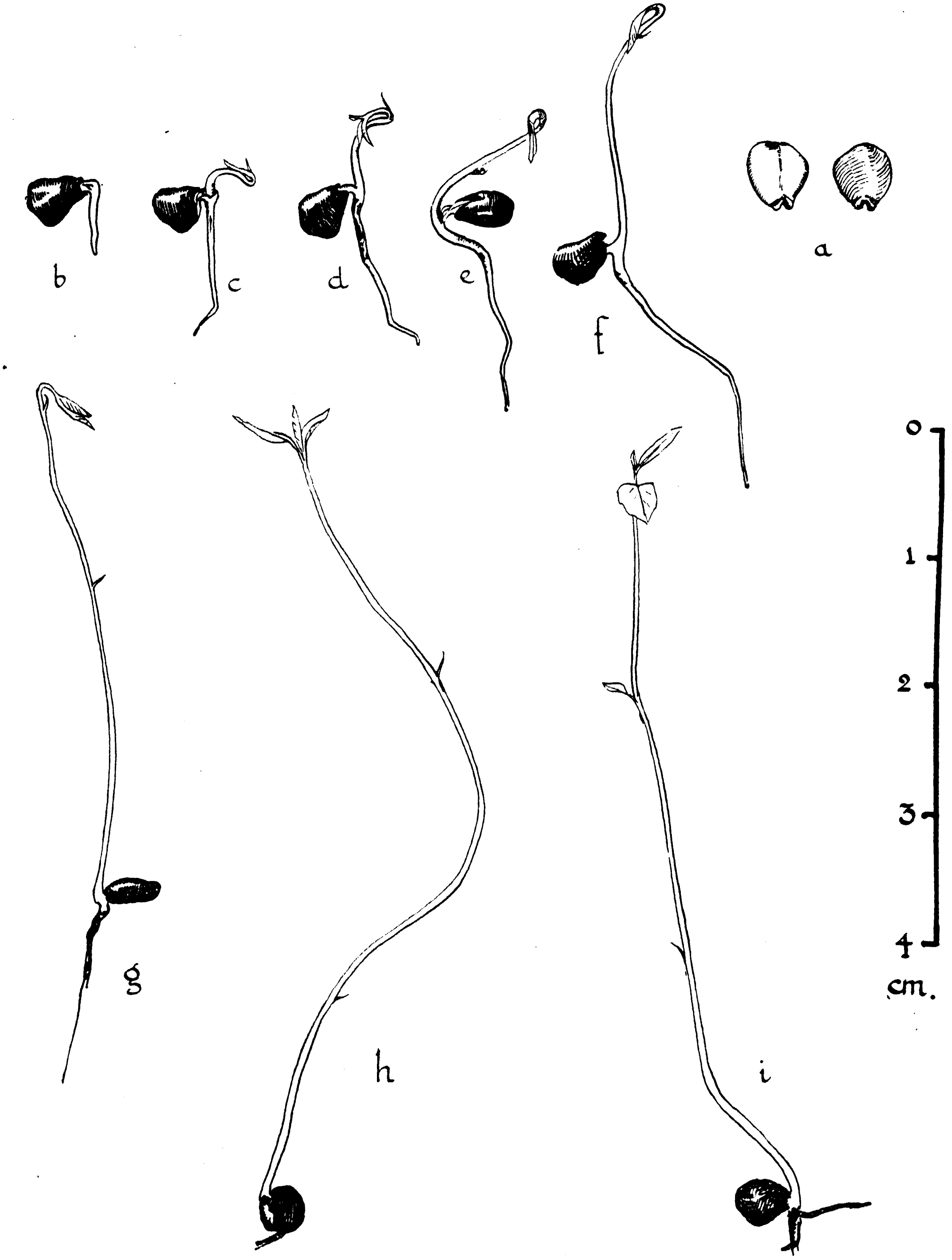

Fig. 2. Stages in germination of *Frangula alnus*, Wicken Fen, June.

In general *Frangula alnus*, although a species tolerant of moderate soil dryness, is characteristic of the moister soil types and situations, showing preference for seepage lines on mineral soils and very frequently associated with gley soils: it is also characteristic of both alkaline, neutral and acidic peat. In none of these situations will it survive permanent waterlogging. It avoids the driest habitats, especially chalk downs and dry limestones, so that possibly it has higher moisture requirements on basic than on acidic soils (P. W. Richards). It seems to be favoured by peat and possibly demands some peat or humus content in the soil. It is on the whole intolerant of shade, and occurs as under-

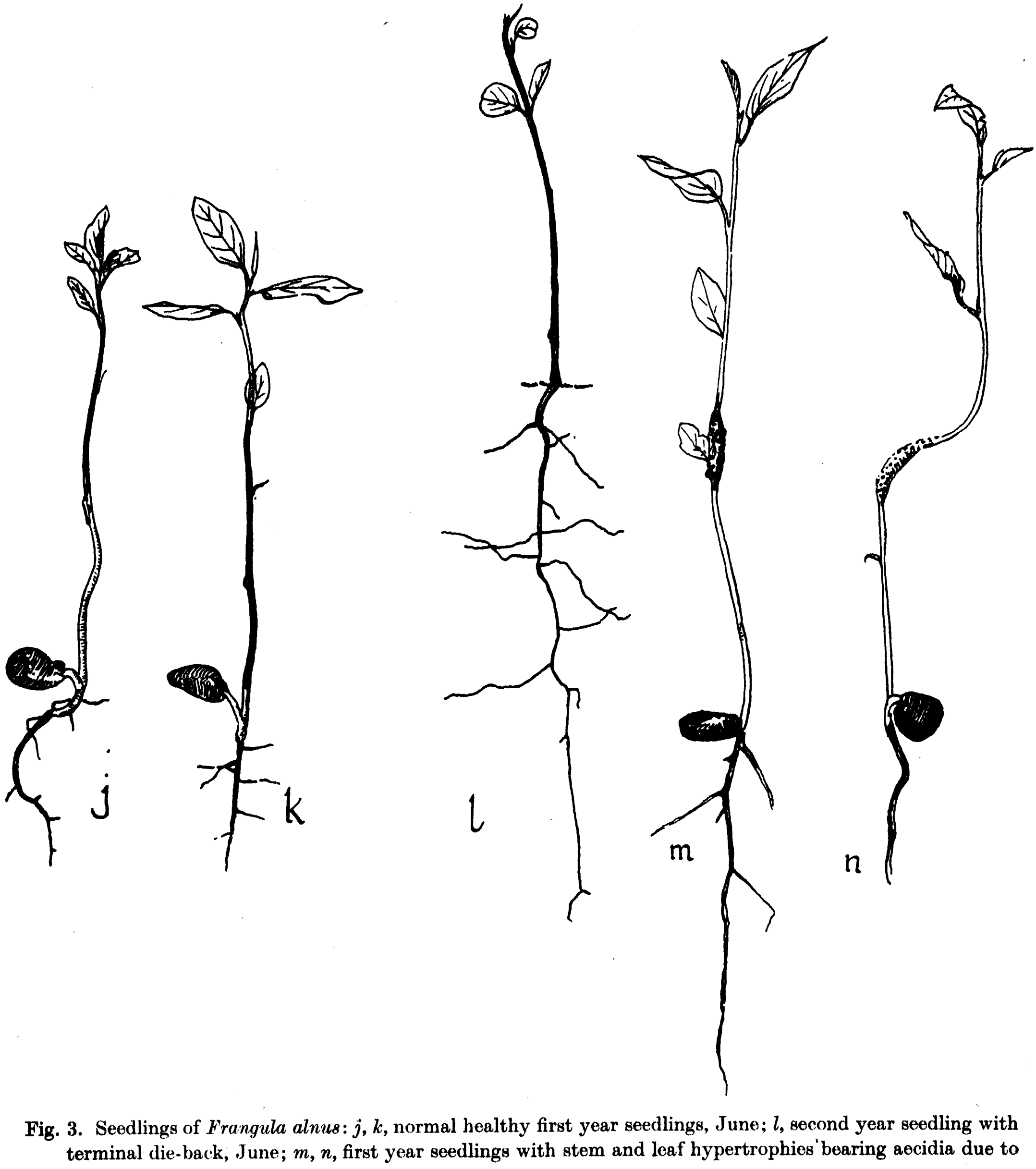

Fig. 3. Seedlings of *Frangula alnus*: *j*, *k*, normal healthy first year seedlings, June; *l*, second year seedling with terminal die-back, June; *m*, *n*, first year seedlings with stem and leaf hypertrophies bearing aecidia due to *Puccinia coronata*, June.

growth therefore only in open woods: it is very typically marginal and seral in its occurrence. In late stages of seres it is killed out by developing tree growth, and it may be present for a short time only in a woodland sere, so that local floras may soon be out of date in records of its distribution. Mass colonization seems due to historical effects of biotic factors rather than to edaphic causes (see IV). It may become abundant in mixed scrub on heavy clay soils after forest clearance and abandoning of coppicing or grazing.

(1) *Alkaline fen peat* (Wicken Fen): soil data as for *Rhamnus cathartica* (see p. 72). Samples of the surface peat round *Frangula* seedlings gave *p*H values 6·0–7·5, and litter round their roots gave values 6·5–8·3 (R. H. Mobbs) (Wicken Fen, using indicator methods).

Light intensity in Fen carr of different seral stages, as percentage of July sunshine in open (Bharucha) (estimates by actinic paper)

Density of carr	Height in m.	Bushes per 24 sq. m.	Age of bushes years	Light	Undergrowth
a	4·3	83	19–22	5·5	Little or no *Cladium*, but shade flora
b	4·3	81	13–17	5·0	
c	4·0	61	13–23	3·1	
d	4·1	91	19–24	8·3	*Molinia*
e	3·5	95	17–20	5·0	A good deal of *Cladium* and *Molinia*
f	3·9	97	13–21	5·0	
g	3·7	103	21–26	5·9	
h	2·7	126	7–11	20·0	Much *Cladium*, *Phragmites* and *Molinia*

Transpiration in midsummer by Franguletum carr at Wicken caused daily lowering of 7–16 mm. in soil water-level, corresponding with transpiration rate of the order of 350–800 ml./sq. m./day (Godwin, 1931).

(2) *Margins of raised bogs, drained raised bogs and other acidic peats. Frangula* tends to be marginal on raised bogs, except where drainage and cutting are concerned, and where base-rich water now floods the bog surface (e.g. Somerset 'heaths'). The following are *p*H values for peat soils in Lake District carrs (supplied by W. H. Pearsall; determinations by quinhydrone electrode):

Out Dubs	(Old Betula)	*p*H 3·44
Ullock	(Old Betula)	3·38, 3·44 (at 1 m. 4·33), 3·50
Ullock	(Old carr)	3·80, 4·40,* 4·68
Stable Hills	(Old alder wood)	4·03, 4·04†
Rusland	(Old carr)	4·84, 5·00†
Roudsea		4·72*
Esthwaite	(Old carr)	4·66, 4·79

All these soils were strongly base-deficient and oxidizing: nitrates were present initially in samples marked *, nitrates developed after 4 days in samples marked †, in others nitrates absent.

At Hatchmere, Cheshire, *p*H = 4 (colorimetric) (T. G. Tutin).

(3) *Heaths and commons.* 'In the vast majority of cases on highly base-deficient soils, and especially heavy acid clays, which when uncultivated tend to carry Calluneta or Molinio-Calluneta in the open, Molinieta in the shade of thin scrub or old Pineta, and *Vaccinium myrtillus* in old deciduous woodland' (E. W. Jones).

On low-lying ground at Wisley, Surrey, with impeded drainage, on Bagshot sands over London Clay: *p*H = 4·5, the sands rich in humus and poor in mineral salts (M. A. H. Tincker).

At Silchester Common, Hants, in a range of situations (T. M. Harris): (*a*) Valley bottom, peaty soil, permanently wet, *p*H 4·3–5·8; (*b*) middle slopes, clay loam with a little gleying, *p*H 5·0–6·0; (*c*) top of valley side, dry well-drained gravelly soil with incipient podsolization, *p*H 4·4–5·6. (Determinations by quinhydrone electrode and colorimetric.)

(4) *Fringing scrub in valley bogs.* At Matley bog, New Forest, Hants, the scrub fringe develops at transition from the lower slopes of the dry heath to the flat, generally waterlogged valley floor: *p*H = 5·1, with higher values (5·9) in carr of the valley centre. Carr with *Frangula* in the valley centre at Holmsley Bog, New Forest, *p*H = 6–7. At Greenham Common, Berks, marginal scrub, *p*H = *c.* 5·0; central streamside carr, *p*H = 5·9 (colorimetric, A. R. Clapham).

(5) *Undergrowth in woodland.* Only found in light shade of open woodland such as old Scots pine, or open oakwood. In Herts, though rare, indicative of the lighter woodland soils (Salisbury, 1918*a*).

III. *Communities.* (1) *On alkaline peat.* Characteristic of seral communities. Probably entering primary hydrosere at late Cladietum stage, certainly initiating secondary successions from Cladio-molinietum and Molinietum of deflected successions when the crop-cutting ceases. Characteristically established in extremely dense and pure stands below which the original ground vegetation is rapidly suppressed. Thus in a big stand (50 sq. m.) analysed at Wicken Fen (1928): age *c.* 25 years; height 2·35 m.; bushes per 50 sq. m.—*Frangula alnus* 67, *Rhamnus cathartica* 1, *Salix repens* var. *fusca c.* 4; living stems per bush, 4; ground-flora living shoots per sq. m.—*Phragmites* 8–30, *Cladium mariscus* 0–53, *Lysimachia vulgaris* 0–3, seedling *Frangula alnus* 0–18, together with *Hypnum cuspidatum* and *Mnium affine.* As carr ages this undergrowth is killed out, *Cladium* often remaining in dense sheaves in *Frangula* crotches with no living plants on ground. Next stage shows much bare ground, non-flowering shoots of *Lysimachia vulgaris, Lythrum salicaria, Symphytum officinale,* and extension of *Thelypteris palustris.* At this stage there may be opening of the canopy by die-back of the *Frangula*, and some expansion of *Rhamnus cathartica*: development of undergrowth of *Agrostis stolonifera, Filipendula ulmaria, Iris pseudacorus, Lysimachia vulgaris, Lythrum salicaria, Phalaris arundinacea, Rubus caesius, Symphytum officinale, Thelypteris palustris, Urtica dioica* (none flowering).

Shrubs commonly associated with *Frangula alnus* in these seres at Wicken Fen are *Rhamnus cathartica, Salix atrocinerea, Viburnum opulus, Crataegus monogyna,* and less often *Ligustrum vulgare, Prunus spinosa,* etc. Old carr of *Frangula* is succeeded by *Rhamnus cathartica* (see p. 72), or potentially by *Quercus robur* and *Fraxinus excelsior.* The character of the shrub stages depends much on initial density of colonization (Godwin, 1936). Open peat surface in Franguletum very densely carpeted with seedling *Frangula* which does not persist beyond 1 or 2 years.

As scattered undergrowth bushes, together with *Rhamnus cathartica,* in *Alnus-Betula pubescens-Salix atrocinerea* carr of Norfolk Broads (Pallis, 1911): see list for *Rhamnus cathartica,* p. 73.

At Holmsley Bog, New Forest, Hants (A. R. Clapham): just below flush from shelly beds, on alkaline peat 1 m. deep there is a patch of carr, with core of *Quercus robur, Ilex aquifolium* and *Taxus baccata* (up to 12 ft. (3·7 m.)), surrounded by *Salix atrocinerea, Prunus spinosa, Ulex europaeus, Frangula alnus, Viburnum opulus* and *Myrica gale.* Ground flora: *Filipendula ulmaria, Primula vulgaris* (f.), *Hedera helix* (v.a.), *Cirsium palustre, Viola riviniana, Potentilla fragariastrum, Phragmites* (o. and marginal).

(2) *Natural margins of raised bogs, drained raised bogs and other acidic peats. Hatchmere,*

Cheshire (T. G. Tutin). In fringe of damp oakwood with *Sphagnum* ground vegetation, where this displaces *Salix atrocinerea*, following *Phragmites* in zones round lake.

North Lancs (W. M. Rankin, 1911). Associated with *Betula*, *Myrica gale*, *Phragmites communis*, *Valeriana officinalis*, *Galium uliginosum*, *Carex gracilis*, *Sphagnum* spp.

Cheshire (E. Price Evans). *Frangula* grows sparingly in woods and copses (*Betula*) on the mosses and raised bogs and about their margins. At Warburton Moss:

Trees		Undershrubs		Ground flora	
Betula pubescens	d.	Betula	l.d.	Pteridium aquilinum	l.d.
Pinus silvestris	o.	Alnus glutinosa (edges)		Deschampsia flexuosa	d.
Quercus robur (and hybrids)	o.	Rhododendron sp. (planted)		Dryopteris dilatata	f.
Pyrus aucuparia	r.	Frangula alnus	o.	Galium saxatile	f.
Alnus glutinosa	r.	Rubus sp.	o.-f.	Rumex acetosella	l.d.
		Pyrus aucuparia	r.	Digitalis purpurea	f.-o.
		Rosa sp.	r.	Epilobium angustifolium	o.
		Corylus avellana	v.r.	Poa annua	o.
		Ulex europaeus	v.r.	Holcus lanatus	o.
		Sambucus nigra	v.r.		

Lake District Woodlands (W. H. Pearsall) (Ullock, old carr; Stable Hills, old alder wood; Rusland, old carr; Roudsea; Esthwaite, old carr). Tree percentages: *Betula* 25–30, *Frangula* 11–22, *Salix* 4–55, *Viburnum opulus* 0–12, *Fraxinus* 0–8, *Pinus* and *Quercus* rare.

Ground vegetation (frequency in 10 quadrats of 1 sq. m.):

Constants:

Eurhynchium praelongum	9
Molinia caerulea	8 l.a.
Filipendula ulmaria	10 l.a.
Athyrium filixfemina	4 (higher figure gives truer frequency)

Other species:

Phalaris arundinacea	4	Rubus fissus	2
Deschampsia caespitosa	5	R. idaeus	2
Solanum dulcamara	4	Valeriana sambucifolia	3
Viola palustris	4	Iris pseudacorus	2
Agrostis alba	4	Galium palustre	2
Dryopteris spinulosa	4	G. aparine	2
Lychnis dioica	4	Lycopus europaeus	2
Hypnum cuspidatum	4	Thuidium tamariscinum	2
Sphagnum spp.	4	Succisa pratensis	1
Holcus lanatus	1	Urtica dioica	1
Pellia epiphylla	1	Brachythecium purum	1

Ullock 'Old Betula'. Tree percentages: *Betula* 50, *Frangula* 35, *Pyrus aucuparia* 5, *Pinus* 7·5, *Quercus sessiliflora* 2·5.

Ground vegetation (frequency in 3 quadrats of 1 sq. m.):

Vaccinium myrtillus	3 l.a.	Plagiothecium undulatum	2 f.
Molinia caerulea	3	Polytrichum formosum	1
Dryopteris dilatata	2	Hypnum cupressiforme	1
Dicranum majus	2 l.a.	Hylocomium loreum	1 f.
Hypnum schreberi	2 l.a.	Thuidium tamariscinum	1
Sphagnum spp.	2		

(3) *Heaths and commons. Oxshott Heath.* Oak-birch heath invading Callunetum on Bagshot sand (V. S. Summerhayes):

Betula alba (dominant)
Quercus robur
Castanea sativa
Pinus silvestris
Calluna vulgaris (scattered)
Erica cinerea (scattered)
Pteridium aquilinum (scattered)
Frangula alnus (few)
Molinia caerulea (not healthy)
Hypnum cupressiforme
Dicranum scoparium

Near Wisley, Surrey. Bagshot sand over London Clay (M. A. H. Tincker):

Quercus sessiliflora
Betula sp.
Molinia caerulea
Erica tetralix
Frangula alnus

North-west Norfolk, in carrs on lower Greensand (C. P. Petch):

Betula sp.	a.	Molinia caerulea	a.
Myrica gale	a.	Holcus mollis	a.
Salix aurita	a.	Hydrocotyle vulgaris	a.
Quercus robur	l.a.	Menyanthes trifoliata	l.a.
Frangula alnus	f.	Phragmites communis	f.
Lonicera periclymenum	f.	Juncus sp.	f.
Rubus fruticosus (agg.)	o.	Thelypteris palustris	f.
R. idaeus	o.	Mentha aquatica	f.
Cirsium palustre	f.	Lotus uliginosus	f.
Lycopus europaeus	f.	Carex goodenowii	r.
Carex paniculata	f.	Viola palustris	r.
Galium uliginosum	r.	Aira flexuosa	o.
Calamagrostis lanceolata	o.	Juncus conglomeratus	o.
Dryopteris dilatata	o.	Succisa pratensis	o.
Angelica sylvestris	o.	Ranunculus flammula	o.
Valeriana dioica	o.	Solanum dulcamara	o.

Silchester Common. North Hants (T. M. Harris):

Wet valley bottom		Drier valley top on gravel and clay	
Alnus glutinosa	a.	Scrub of Quercus robur	
Salix atrocinerea	a.	Ulex europaeus	
Quercus robur	f.	Pteridium aquilinum	
Viburnum opulus	f.	Erica cinerea	o.
		Calluna vulgaris	o.
		Vaccinium myrtillus	o.

South Haven Peninsula (C. Diver). Chief species associated, *Erica tetralix, Molinia caerulea, Calluna vulgaris.*

Ditchling Common, East Sussex, on Weald Clay (P. W. Richards):

Prunus spinosa	f.	Corylus avellana	o.	Crataegus	f.
Ulex europaeus	l.f.	Quercus robur	f.	Betula sp.	l.f.
Salix caprea	o.	Viburnum opulus	r.	Frangula alnus	f.
S. atrocinerea	a.	Pyrus malus	o.		

In similar scrub areas on heavy clay associated also with *Acer campestre, Fraxinus excelsior, Rosa* spp., *Rubus fruticosus* agg., *Lonicera periclymenum.*

(4) *Fringing scrub in valley bogs.* Beside the wide shallow valley bogs of the New Forest there is often a narrow, discontinuous scrub fringe at the junction of dry heath and valley bog. *Matley Bog* (A. R. Clapham):

Molinia caerulea	c.o.-d.	Festuca ovina	o.-l.a.	Especially in upper part of zone
Myrica gale	c.o.-d.	Luzula campestris		
Frangula alnus	f., l.a., l., c.o.-d.	Erica tetralix		
		Hypnum schreberi		
Ulex europaeus	o.	H. cupressiforme		
Pinus silvestris	o.	Sphagnum spp. (group subsecunda)	v.a.	Only in lower part of zone
Betula alba	o.	Juncus acutiflorus		
Alnus glutinosa	r.	J. bulbosus		
Ilex aquifolia	r.	Carex panicea		
Pyrus malus	r.			
Calluna vulgaris	r.			
Rubus fruticosus	r.			

Salix cinerea	Also enter in some places
S. repens	
Hedera helix	
Lonicera	
Rosa sp.	

Inside this scrub belt lie more or less flooded zones with *Molinia, Juncus acutiflorus, Sphagnum* spp. (group Subsecunda), *Juncus effusus, Glyceria fluitans, Sparganium ramosum* as dominants. Centrally in the bog is alder carr with *Salix atrocinerea* at the edge and outside this a broken fringe of *Frangula alnus* and *Myrica gale.*

(5) *Limestone scrub.* Occurs in the dense Coryletum of west Irish limestone crags with *Euonymus europaeus, Cornus sanguinea* and *Rhamnus cathartica.* On the Burren with *R. cathartica* and other shrubs (see p. 73).

(6) *Undergrowth in woodlands. Frangula,* though very rare, is characteristic of true sessile oakwoods with *Viburnum opulus, Sorbus aria, Ilex aquifolia* (Tansley, 1939). In Essex occasional to locally frequent in old *Quercus robur* scrub which represents a transition to *Q. robur-(sessiliflora)-Carpinus* woodland and, though rare, very characteristic of *Quercus sessiliflora-Carpinus* woods of Herts, as opposed to *Quercus robur-Carpinus* woods on heavier soils (Salisbury, 1918*a*).

Enters in limited amount in the light shade of old Scots Pine wood or light oakwood; typical associates in this habitat are *Calluna vulgaris, Vaccinium myrtillus, Pteridium aquilinum, Molinia caerulea, Deschampsia flexuosa, Pyrus aucuparia, Ilex aquifolia, Crataegus, Viburnum opulus, Prunus spinosa, Acer campestre,* etc.

In the New Forest, Hants; enters young plantations by seed, and occurs as seedlings in 70–80 year old *Pinus silvestris* woods where these become open enough (E. W. Jones). Also in larch and pine plantations (A. R. Clapham).

At Burnham Beeches, *Frangula* is occasional at the wood margin and in openings, in areas where water collects, with *Molinia, Erica tetralix,* Sphagna, *Polytrichum commune, Aulacomnium palustre, Betula* and *Populus tremula* (A. R. Clapham). In the narrow valley oakwoods beside Dartmoor: scrubby *Quercus robur* and *Q. sessiliflora* about 20–30 ft. tall, *Frangula* is a thin undergrowth with ground flora of *Lonicera periclymenum, Melampyrum. Luzula sylvatica,* and *Stellaria holostea.*

At Windermere, north Lancs, 200 ft. O.D., on Bannisdale Slate (T. G. Tutin):

Betula alba	d.	Vaccinium myrtillus	f.	Mnium hornum	f.
Quercus robur	f.	Lathyrus montana	o.	Thuidium tamariscinum	
Alnus glutinosa	o.	Hieracium sp.	o.	Polytrichum formosum	
Corylus avellana	d.	Solidago virgaurea	o.	Dicranum majus	
Fraxinus excelsior	o.	Holcus mollis	f.	Hypnum cupressiforme	f.
Lonicera periclymenum	f.	Rubus sp.	o.	Diplophyllum albicans	
Frangula alnus	r.	Teucrium scorodonia	o.	Lepidozia reptans	

In Continental Europe occurs in open deciduous woodland with *Alnus incana* and *Corylus avellana*, in hedges and wood margins, 'sowohl auf kalkreichem als auf völlig kalkfreiem Boden'. With *Salix cinerea* one of the first pioneers of peat mires. Favours shadier and damper situations than *Rhamnus cathartica* (Braun-Blanquet & Rübel, 1932–6). Common as undergrowth in *Alnus glutinosa* fenwoods, often persisting from an earlier seral scrub stage (*Weiden-Faulbaum Gebusch*), which invades *Molinia* and *Schoenus* meadows (e.g. Schoenichen, 1933). Frequent in *Pinus-Betula* woods of *Zwischenmoorwälder*, and in similar tree growth beside drainage channels of raised bogs in north-west Germany (Steffen, 1931). Common in hedges, and in alpine regions on the heaps of stones collected from the fields. Described by Hegi as extending to very dry soils, although the driest cited has *Calluna* undergrowth. As undergrowth in mixed woodland of oak and conifer on lighter soils (Graebner, 1933). In Normandy enters freely into young crops of *Quercus*, *Pinus*, etc., and persists in small amount in old deciduous or coniferous woodland. Here as in Vosges and Black Forest on various soil types up to 700 m. (E. W. Jones).

IV. *Response to biotic factors.* Colonization is suppressed by sedge-cutting and litter-cropping at Wicken Fen, but very rapidly follows removal of the deflecting factor. Regenerates very strongly indeed from stools after cutting, burning, and grazing, and therefore very resistant to these factors: in England strikingly characteristic of grazed and burnt commons. Mass colonization, which often leads to dense pure communities of *Frangula*, probably follows from some disturbance due to biotic causes, such as burning, clearing, cessation of grazing or cropping. Strongly characteristic of marginal zones, e.g. margins of woods, commons, heaths and raised bogs, which may reflect the seral character of its commonest occurrences, and its dispersal by birds.

Molisch (1909) reports that shoots can readily be made to sprout in the resting season by a warm bath (35–40° C.), followed by keeping in a cool greenhouse.

V. (*a*) *Gregariousness.* Rather strongly gregarious, depending on density of seed dispersal and response to conditions suitable for ecesis.

(*b*) *Performance in various habitats.* Commonly as a many-stemmed bush up to 13–16 ft. (4–5 m.) tall, but when older forming a small tree. Exceptionally up to 52 in. (1·32 m.) in girth at 33 in. (0·80 m.) from ground (by R. Dart near Newbridge, Devon), and 39½ in. (1·00 m.) girth (Skinner's Wood, Shapwick, Somerset), but in the latter instance only 32 annual rings in an average wood radius of 6 in. (15 cm.): remarkably rapid growth.

Bushes in deep shade are of very open diffuse habit and the leaves are larger, thinner and less rigid than sun leaves.

(*c*) *Effect of frost, drought, etc.* Seedlings on peat soils suffer from frost heaving. Prolonged submersion when buds are dormant or when leaves are open does not appear to damage seedlings, but during active phase of spring leaf expansion seedlings are seriously injured or killed if totally submerged for a few weeks. There is some indication that this is the mechanism restricting invasion of wetter habitats in Wicken Fen (Godwin & Bharucha, 1932). In dry situations leaf development is poor and narrow dull-surfaced leaves are prevalent, also almost all flowers fall without setting fruit. Sunleaves are relatively broader and more shiny than shade leaves.

VI. (*a*), (*b*) *Morphology, etc.* On alkaline peat the whole root system is in the top few centimetres of soil above the water-table.

(*c*) *Mycorrhiza.* The whole root system both in seedling and mature plant is mycorrhizal; in effect all young functional roots are mycorrhizas. The association is endotrophic with a member of the arbuscular-vesicular group of fungi. The mycelium is both intercellular and intracellular in distribution, the intercellular mycelium conspicuously abundant, affecting the whole of the cortical tissues.

Large pear-shaped vesicles are frequent (in material collected in October), and the intracellular complexes undergo digestion giving rise to a characteristic sporangiole phase. In older roots all the intracellular mycelium is in this phase (M. C. Rayner, report on plants from alkaline peat, Wicken Fen).

(*d*) *Perennation.* Deciduous microphanerophyte without scales on winter-buds.

(*e*) *Vegetative reproduction.* Unrecorded.

(*f*) *Longevity.* Not known.

(*g*) *Age at first flowering.* Flowers and fruit formed very early.

(*h*) *Frequency of seed production.* In southern Britain seed is set very freely indeed every year.

(*i*) *Ecotypes.* Unreported, although it has been suggested that the populations of acid and alkaline soils may show hereditary morphological differences.

(*j*) *Chromosomes.* $2n=20$ (D. G. Catcheside).

VII. *Phenology.* (*a*) Time of maximum root growth not known.

(*b*) Leaves first appear in early April and late May (Wicken, Conway, 1934, 1935; Godwin, 1928, 1931, 1941). Leaves yellow and fall in October (Wicken, Godwin, 1927; Conway, 1934).

(*c*) Flowering begins in late May and June, often but not always continuing through June and July to end of season (August, September) along with ripening fruits (Wicken, Conway, 1934; Somerset from 1933, Watson). Flowering probably arrested by low autumn temperatures.

(*d*) Fruits first reddening in July and some black in mid August: large proportion black by end of August. Mostly ripe and falling in September, October, November. Few persist on bushes in December.

(*e*) Germination abundant in spring in wet surface litter of Cladieta, Cladio-Molinieta, and Rhamneta, especially below parent trees; sometimes in axils of dead *Cladium* leaves, rootlets reaching peat soil through dead leaf remains; frequently in dense clumps from abandoned mouse stores.

VIII. (*a*) *Mode of pollination.* Flowers bisexual, insect pollinated: the pale green petals enclose the short stiff stamens and are somewhat smaller than the sepals, which persist and fold inwards after fertilization. The receptacle forms a deep funnel-shaped cup which serves as a nectary and the stamens bend inwards leaving only a small central entrance directly over the stigma. The flowers are said to be protandrous, and in some places to be of two types, long and short styled on different races (Schulz, 1888–90). If insect pollina-

tion fails, self-pollination is said to occur: the stigma is a very short distance below the anthers. The flowers are very freely visited by bees, both hive-bees and bumble-bees (British as well as continental records), and in addition by wasps, ichneumon flies and beetles.

Continental records include:

HYMENOPTERA

APIDAE: *Apis mellifica* L., *Bombus agrorum* F., *B. jonellus* K., *B. proteus* Gerst., *B. terrestris* L.

VESPIDAE: *Vespa silvestris* Scop., *Eumenes pomiformis* L., *Polistes gallica* L.

COLEOPTERA

Corymbites sjaelandicus Müller, *Elater balteatus* L., *E. pomonae* Steph., *Sericus brunneus* L.

MUSCIDAE

Lophosia fasciata Mg.

Judging by the fruiting of isolated bushes, the species must be self-fertile.

Only exact personal records available for Britain are the following by O. W. Richards (Cot Hill, Berks, 6 June 1926):

HYMENOPTERA

APIDAE: *Andrena pubescens* Oliv., *A. jacobi* Perk, *A. barbilabris* (Kby.), *A. haemorrhoa* (Fab.), *A. saundersella* Perk., *A. dorsata* (Kby.), *A. synadelpha* Perk., *Halictus fulvicornis* (Kby.).

DIPTERA

SYRPHIDAE: *Criorrhina oxyacanthae* (Mg.), *Orthoneura brevicornis* Lw., *Chrysogaster hirtella* Lw., *Cnemodon vitripennis* (Mg.).

MEGALOPTERA

RAPHIDIIDAE: *Raphidia xanthostigma* Schumm.

COLEOPTERA

OEDEMERIDAE: *Ischnomera coerulea* (L.).

DERMESTIDAE: *Attagenus pellio* (L.).

Of the bees, *Andrena haemorrhoa* was the commonest, while several of the others were in large numbers. *A. synadelpha* is the only one which seems to have a definite preference for *Rhamnus*. There is also one record of visitation by *Bombus terrestris* (Leatherhead, 7 July 1942, I. H. Burkill).

(*c*) *Cleistogamy*. Unreported.

(*d*) *Apomixis*. Presumably amphimictic.

(*e*) *Vivipary*. Not recorded.

(*f*) *Hybrids*. Not recorded.

(*g*) *Amount of seed*. Usually two pyrenes per fruit. Bushes fruit heavily, e.g. a many-stemmed bush 7 ft. (2·1 m.) tall, bore 1804 fruits on 27 September 1932 (Godwin, 1936), but in dry situations flowers drop and the crop is small.

(*h*) *Dispersal.* Birds, mice and simple falling to the ground are all important agents in dispersal, and Woodruffe-Peacock writes that 'it is bird-sown on all our lines of migration' (i.e. near Cadney, Lincs). In late September great flocks of field-fares (*Turdus pilaris* L.) feed on the ripe fruits at Wicken Fen, and the purple-stained excreta are abundant on the reeds. In addition missel-thrush (*Turdus viscivorus* L.) (C. Raven) and pheasant (*Phasianus colchicus* L.) (Wm. Barnes) take fruit at Wicken. In Alpine valleys characteristic of collected stone-heaps, '*Mutschnahügeln*' were voided by birds along with many similar species.

In shallow runs in the peat at Wicken Fen, field-mice collect the pyrenes and stores of them, 30–100 in number, often germinate to give a compact tuft of seedlings. *Apodemus sylvaticus* L. was seen to collect and eat the stones, leaving the characteristic arillar portion. The extracted dry stones placed on a tray at ground-level were rapidly removed by mice, and stones were taken from whole fruits in the tray as soon as drying caused the fruits to crack and expose the pyrenes. Extracted pyrenes on a tray out of reach of mice were slowly removed, presumably by birds, but the whole detached drupes were not. Pyrenes planted below surface of fen peat were also discovered and eaten by mice (Godwin, 1936).

Between September and December the fruits fall freely from the bushes, and seedling establishment beneath adult bushes is consequently very dense (order of 100 seedlings per sq. m.). On recorded bush at Wicken Fen, of 1804 fruits present on 27 September 1932, 1268 had fallen to the ground by 24 December, and only about 500 had disappeared (presumably taken by birds).

Praeger (1913) reports that the whole fruits float for 2 weeks and seeds for 1 week, but positive evidence of water transport is lacking despite the water-side habitats in which the plant grows.

(*i*) *Viability.* At least 3½ years (Kinzel, 1926).

(*j*) *Conditions for germination.* According to Kinzel (1926) the seeds need a rest of about 6 months, and germinate only in light: dark germination requires frost and both light and frost accelerate germination. Kinzel's observation that natural germination takes place in the spring following shedding is confirmed at Wicken Fen, but his other observations may need qualification. Thus pyrenes extracted from ripe fruits and sown within a few days either in peat or in Petri dishes give a high percentage germination (over 75%—Godwin, 1936; Bharucha, 1932). After being left dry for a longer time the pyrenes exhibit a dormancy which can be broken by cutting through the endocarp. After several months' drying it is difficult to secure any germination (note maintained wetness of peat soils and soil moisture of other habitats).

(*k*) *Morphology of seedlings.* Emergence of small brown radicle to one side of the two arillar lumps is followed rapidly by pale yellow hooked epicotyl which rapidly extends, still hooked, 1 or 2 cm. above ground-level. Epicotyl bears one or two very small prophylls: leaves of terminal hook folded along mid-rib become green when only a few mm. long, show serrate margin and, like the stem, have a sparse covering of short curved hairs. As seedling ages the stem of the epicotyl becomes green, then pink or red, and leaves thicken, darken, become shiny and veins project on lower surface. Seedlings found naturally on alkaline peat had no root hairs on primary or lateral roots. Obovate cotyledons remain yellow-green inside non-endospermous seed and hard endocarp of pyrene remains unsplit, or split very little, and attached to seedling for several months. Within a short time after germination many seedlings show hypertrophy due to *Puccinia* (see Fig. 3 *m, n*). A very large proportion of older seedlings shows die-back of apical shoot and growth continued from a lateral. Leaves have minute stipules which turn brown and are shed early.

(*l*) *Effective reproduction.* Entirely by seed.

Table of striking morphological and ecological differences between the two buckthorns

		Rhamnus cathartica	*Frangula alnus*
Stems	i	Spinous	Unarmed
	ii	Regular branches in pairs at right angles	Less regular and at smaller angle
	iii	Rough with bases of dead lateral stems	—
	iv	Abundant dwarf flowering shoots	Flowers in small axillary groups on young wood
	v	Young wood of shoots whitish	Young wood dark brown
Bark	i	Scaling	Smooth and peeling off dead wood
	ii	Blaze orange	Blaze lemon-yellow
Buds	i	With bud scales	Naked with fine brown hairs
Leaves	i	Ovate	Obovate with pointed apex
	ii	Serrate	Entire (but wavy) margin
	iii	Dull green, downy beneath	Shining surface
	iv	Veins strongly converging	Parallel veins
	v	Become yellow before falling	Bright yellow and red in autumn
Flowers	i	Tetramerous	Pentamerous
	ii	Dioecious	Bisexual
	iii	Cleft stigma	Entire stigma
Fruits	i	Green to black on ripening	Green to red to violet-black
Pyrenes	i	Usually 3–4 per drupe	Usually 2
	ii	Obovoid with triangular cross-section, furrow small and along inner edge of base	Compressed, broadly obovoid with deep furrow formed by two humps projecting through endocarp
Germination	i	Epigeal with 2 green persistent cordate cotyledons	Hypogeal
Rootlets	i	Pale in colour	Bright orange
Distribution	i	Has more pronounced south-west limitations	Extends somewhat further north in Europe
	ii	Somewhat greater altitudinal range	—
Habitats	i	Strong calcicole preferences }	Avoids dry soil in general, especially limestones
	ii	Extends to drier habitats }	
	iii	—	Somewhat more shade tolerant
Flowering	i	Restricted flowering season	Very extended
Fruiting	i	Fruits persist on bushes; possibly unpalatable	Fruits fall easily; readily bird dispersed
Germination	i	Freer and over long season	Restricted and seeds readily becoming dormant
Habit	i	Rather dense crown	Very diffuse habit especially in shade
Disease	i	—	Very susceptible to die-back

IX. *Parasites: diseases.* See composite lists for two buckthorns in table above.

Throughout Wicken Fen bushes of all ages suffer from a terminal die-back (see Fig. 3 *l*). In mature Franguletum in some years this may be so widespread and serious as to affect materially the dominance of *Frangula*, and favour extension of *Rhamnus catharticus*, which does not suffer in this way: opening of the canopy also affects the undergrowth. Entry of the parasite appears often to be through the bases of dead lateral branches.

X. *History.* Recognized in Interglacial beds at Hoxne and West Wittering (Reid, 1898), in west Germany with *Brasenia purpurea*. Constantly present in small amounts in the last Danish interglacial deposits (Jessen & Milthers, 1928).

Present in several Neolithic lake settlements in Switzerland (Früh & Schröter, 1904) and in Neolithic of Sweden (Reid, 1898), but Jessen (1930) reports for Denmark: 'The oldest Post-glacial finds date from the early part of the mixed-oak forest: this shrub, however, as in Sweden and Norway, immigrated in the early part of the pine period.'

Identified by Clifford at Woodwalton Fen, Hunts, at top of fen wood peat at levels just below maximum extension of fen clay, i.e. Neolithic, in Pollen Zone VII (Godwin & Clifford, 1938).

XI. *Uses.* It has been long recognized that the wood yields the highest quality charcoal for gunpowder: the shrub was formerly planted to ensure this supply. Bark and berries have been used as purgatives in folk medicine, and the bark has been an official drug in Germany since the middle of last century. Bark, leaves and unripe fruits were used to obtain the dye sap-green. On the continent Hegi (1925) reports the use of seeds to yield a burning oil, shoots in besoms and as withies, and the hard wood for teeth, pegs, turnery, inlaying, etc. He also cites 'Butcher's prickwood' as an English name: 'Alder-buckthorn' and 'Black dogwood' are commoner names.

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BRITISH ECOLOGICAL SOCIETY

MEMORANDUM ON NOMENCLATURE AND TAXONOMY IN THE BIOLOGICAL FLORA

NOMENCLATURE

The absence of a recently published authoritative hand-list of British Flowering Plants raises the troublesome problem of nomenclature in the Biological Flora. It is the wish of the Council of the British Ecological Society that the names used should be in accordance with the International Rules of Botanical Nomenclature. The Editorial Committee, with the help of its taxonomic advisers, will be pleased to advise contributors on nomenclatural matters, and will check the names used by them.

The Council have, however, decided to depart from the Recommendation in the International Rules that specific epithets which are old generic names or derived from personal names or vernaculars should be spelt with initial capitals. While the Council are most reluctant to take any course which may delay a full agreement on questions of nomenclature, they feel most strongly that there are inadequate grounds for the retention of initial capitals in specific epithets, and that the arguments for discarding them completely are very strong.

For the retention of initial capitals by far the most weighty argument is that a responsible botanical society should further standardization of nomenclature by following any rules or recommendations upon which the representative international body has been able to agree. There is an understandable distaste for seeing personal names written with small initials, and it is perhaps of some interest to be able to recognize a specific name as that of an old genus; but these are largely matters of sentiment. The convention may obviate confusion where a noun in apposition fails to agree in ending with its generic name, but many of the old generic names recur (*Saxifraga*, *Cymbalaria* etc.), and the student soon learns that they are to be excused conformity.

In favour of discarding all initial capitals in specific epithets there are the following arguments: that the recommended practice maintains an unnecessary and undesirable source of error which squanders the time of students, teachers and editors; that it may be difficult to decide whether an epithet has even been used as a generic name; that zoologists have already discarded all such capitals; that the opposition to the practice is too strong to secure its general observance, and some important groups of taxonomists (e.g. the Washington Group in U.S.A.) ignore it consistently; and that a work of such large scope as the Biological Flora, appearing over a long period, may usefully exert its influence in favour of changing the recommendation.

TAXONOMIC UNITS

The Council attach importance to the establishment of uniformity in the nomenclature of intraspecific units. They realize that it is impossible, with the incomplete knowledge of to-day, to attempt to describe and define all the different kinds of intraspecific units which may be required for an adequate systematic treatment of British Flowering Plants. They nevertheless set out the following statement of the practice which the Editorial Committee recommend in order to prevent different contributors from attaching widely different meanings to the same terms.

Species. Groups referred to as species should be clearly differentiable by a sufficient number of highly correlated characters. In general, it seems best that the Biological Flora should aim at a mean between extreme 'lumping' and extreme 'splitting'. Contributors may find it useful to recognize different kinds of species (cf. the coenospecies, ecospecies and agamospecies of Türesson; and see below).

Subspecies (subsp.). This term should be used for morphologically distinguishable intraspecific groups which are more or less isolated by geographical, ecological, cytogenetical or other barriers to general cross-breeding, but are less clearly distinct than are species, 'intermediates' occurring more frequently or over a wider area. The term should only be used after a very full consideration of all available facts and not merely as a way out of a taxonomic difficulty. Many of the subspecies of British Floras are better treated as separate species.

Some contributors may wish to recognize kinds of subspecies differing in the operative isolating mechanism (see below).

Variety (varietas: var.). This term should be used for all intraspecific groups which cannot be regarded as subspecies or forms (see below), and for all which are of unknown status.

Form (forma: f.). The term should be applied to groups of individuals which differ from other groups in characters which there are good reasons for supposing to be non-heritable; e.g. the land and water forms of *Polygonum amphibium* L.

These four terms are in common use by taxonomists, though unfortunately with much diversity of meaning. Contributors to the Biological Flora will find it necessary, as ecological and cytogenetical knowledge increases, to recognize several more or less distinct kinds of varieties amongst those of known status. The following terms should be confined to the meanings here given; further research may show that additional terms are needed (cf. the list given by du Rietz in *Svensk. Bot. Tidskr.* **24**, 333 (1930)).

Ecotype[1] (ecotypus: ecot., a term originally suggested by Türesson) may be used for intraspecific units which occupy different habitats and show hereditary and probably selective differences in certain characters, especially of vegetative form and habit and of phenology, though they may show much uncorrelated variation in other characters, particularly in flowers and fruits. They differ from ecologically isolated subspecies in being less distinct and in that the visible differential characters are chiefly vegetative; but the two categories intergrade. An example is the littoral variant of *Juncus articulatus* L. emend. Wahlenb., the individuals of which agree in their characteristic genetically determined dwarf rigid habit but vary between (and often within) populations in many characters of inflorescence, flowers and fruit.

Cytotype (cytotypus: cytot, a term suggested by A. J. Wilmott). This may be used for intraspecific units differing in chromosome number or structure, and perhaps in plant dimensions, but not markedly in other obvious morphological characters; e.g. the diploid, tetraploid, and octoploid variants of *Galium palustre* L. (Hancock, *New Phytol.* **41**, 1942). Cytotypes differ from cytogenetically isolated subspecies in that isolation may be less complete and particularly in that morphological differentiation is slight. They may show certain geographical or ecological differences as well as cytological. When this is so they may be regarded as extreme kinds of ecotypes.

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[1] Dr J. Ramsbottom and Mr A. J. Wilmott object to this and the two following terms as liable to confusion with the set of taxonomic terms, also ending in -type, descriptive of kinds of type specimens. The terms are retained here because 'ecotype' is already firmly established, but by adopting the abbreviations 'ecovar.' etc., suggested by Dr Ramsbottom, the danger of confusion should be removed.

Genetotype (genetotypus: genetot.). This new term should be used for sets of individuals showing similar characters with a genetic basis and distributed more or less at random within the geographical range of a species or subspecies.[1] Since new genetotypes may result from a single gene mutation or from any new combination of genes it follows that the number of genetotypes within a species may be very large indeed. From this it follows that the application to genetotypes of names comparable in taxonomic status with those attached to subspecies is undesirable. Names, when it is necessary to use them, should be applied only as a description of the variant *character*. Such characters may, however, be very numerous and variously combined, and it will clearly be impracticable to provide new Latin names for every combination. It will generally be preferable to indicate the genetic constitution of genetotypes by the use of appropriate symbols rather than by Latin names (cf. the procedure adopted by Marsden-Jones and Turrill for *Silene vulgaris* and *S. maritima* in *Kew Bulletin*, 1929, p. 168 and 1931, p. 136).

Geographical or ecological gradients in characters having a genetic basis will almost certainly be encountered by some contributors. They should be termed 'clines' (term introduced by J. S. Huxley) in the characters in question.

None of the above terms, apart from 'variety', should be used unless the status of the groups in question has been established by appropriate observations and experiments. It is desirable, in order to avoid taxonomic confusion, that the categories defined by the terms ecotype, cytotype and genetotype should be regarded as *varieties* of ascertained status. If named they may be cited as ecovar., cytovar., genetovar., for *varietas ecotypica*, (*cytotypica*, *genetotypica*), where the term *ecotypica* merely qualifies *varietas* and necessitates no nomenclatural change unless perhaps an emendation of the original name by the authority for the kind of variety (ecovar. *prostrata* Smith, em. Robinson).

It is to be noted that there are no clear lines of demarcation between varieties, subspecies and species when, as often, they represent stages in specific differentiation. Kinds of subspecies and species, corresponding with some of the kinds of varieties referred to above but with greater morphological differentiation and more complete isolation, may therefore be distinguished, in an analogous way, as *subspecies* (or *species*) *ecotypicae*, *cytotypicae*, etc., and written ecosubsp., cytosubsp. etc.

Variants already named but of unknown or doubtful status may be referred to thus: 'var. *prostrata* Smith, with prostrate shoots and few-flowered inflorescences, is probably either an ecotype or a non-heritable form, but precise information is lacking'; or 'f. *parviflora* Jones, described as having flowers only half the normal size, has been reported from west Norfolk. Its taxonomic status is unknown.'

Hybrid swarms and sets of apomictic or almost exclusively self-pollinated individuals, such as the segregants from *Centaurea nigra* L. × *C. jacea* L., the numerous apomicts included under *Taraxacum officinale* Weber, and the self-pollinating 'microspecies' (autotypes) of *Erophila verna* (L.) Meyer, cannot yet be fitted into the above scheme. It is suggested that, until a decision can be reached as to the best way of classifying and naming them, it would be better not to give binomial names to such sets. It will often be practicable and convenient to treat them as special kinds of varieties of larger groups (cf. the treatment by Babcock and Stebbins Jnr. of the apomictic polyploid complexes of the genus *Crepis* in North America: *Instn. Publ. Carneg.* no. 504, 1938).

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[1] Members of one genetotype are phenotypically distinguishable and genotypically different from those of other genetotypes, but are not all phenotypically similar, since they include a range of non-heritable forms; and are not likely to be genotypically identical.

That published floras and plant lists may include many taxonomically different types under similar categories is shown very clearly by the following notes supplied by E. M. Marsden-Jones and W. B. Turrill on *Centaurea* species in Druce's *British Plant List*, 2nd ed. (1928): *C. jungens* Gugl. is a first generation hybrid of *C. jacea* L. × *C. nigra* L.; *C. angustifolia* Gugl. is a genetotype of *C. jacea*; *C. pratensis* Thuill., *C. drucei* C.E.Br., and probably *C. surrejana* C.E.Br. are segregants from *C. jacea* × *C. nemoralis* (or other members of the *C. nigra* complex); and *C. obscura* Jord. is *C. nigra* L., but it and *C. nemoralis* may be regarded as subspecies of a single species, with different but overlapping geographical ranges. Of the varieties listed under *C. nemoralis*, var. *diversifolia* C.E.Br. and var. *subintegra* C.E.Br. are genetotypes in the sense suggested above; var. *minima* C.E.Br. is (at least in part) a form (i.e. non-heritable) and var. *microptilon* C.E.Br. is a segregant from *C. jacea* × *C. nigra*. (Date from unpublished and unfinished work. Some of these statements may need modification in detail.)

It is possible that some contributors may wish for advice in dealing with units of particular taxonomic difficulty. The procedure should be first to collect all the relevant facts and then to submit them with specimens and the tentative taxonomic conclusions to the Editorial Committee and its taxonomic advisers. The Council recommend that no taxonomic changes should be made in the first place in the Biological Flora, but that separate papers should be written for appropriate journals such as the *Journal of Botany*.

It is important to emphasize that ecological and taxonomic researches are frequently interdependent, and that by collaboration with taxonomists contributors to the Biological Flora may further the best interests of both branches of botany.

ANNUAL MEETING IN THE UNIVERSITY BOTANY SCHOOL, CAMBRIDGE

5 AND 6 JANUARY 1943

Tuesday, 5 *January*

The winter meeting of the Society commenced in the afternoon of Tuesday, 5 January, with the assemblage of members and guests in the Elementary Laboratory of the Botany School, Cambridge, where a series of exhibits had been set out. These included subfossil specimens of *Meesia triquetra* (L.) Aargstr. from peat on the Somerset Levels, together with recent specimens from Iceland for comparison, put out by Dr P. W. Richards. Mr N. W. Simmonds showed living plants of *Lycopodium inundatum* from St Leonard's Heath, Dorset. Mr T. G. Tutin exhibited a distribution map of *Juniperus communis*, specimens showing different leaf proportion and size, and specimens of wood. Sets of lantern-slides of Spanish plants were shown by Dr H. Godwin, and of the blanket-bog of Dartmoor by Dr H. Hamshaw Thomas. Dr Godwin set out a series of types of peat found in coastal exposures, together with pollen diagrams and specimens from the peat of the Somerset Levels. Two pollen diagrams served to date prehistoric trackways, from one of which were exhibited stakes of *Fagus sylvatica*. Miss A. Conolly showed fossil leaves of *Salix herbacea* from layers presumed to be of *Allerød* age in a Cornish kaolin pit. Dr K. B. Blackburn put out exhibits illustrating (i) peat investigations on the Isle of Soay, which offer the chance of dating the maximal transgression of the sea in that part of Scotland, (ii) sterile hybrid plants of *Limosella aquatica* × *L. subulata*, and the fertile amphidiploid ($2n=60$) derived from the first by treatment with colchicine, and (iii) a series of peat types and pollen diagrams from a site at Neasham near Darlington, where there had been found a skeleton of an elk, *Alces alces*. After tea in the laboratory the meeting adjourned.

Between 80 and 90 members and guests were present at a soirée held the same evening in the Combination Room of Clare College. At the close of a most enjoyable social gathering, Prof. Osborn expressed the thanks of the Society to the Master and Fellows for the use of the Combination Room, and to the ladies who had provided the generous tea at the afternoon meeting. The meeting dispersed about 11.0 p.m.

Wednesday, 6 *January*

At 10.0 a.m. the General Meeting opened in the Cambridge Botany School, the President in the chair. Regrets for absence were reported by L. A. Harvey, W. B. Turrill, M. A. H. Tincker, R. Ross, C. Diver, E. Wyllie Fenton, and W. H. Pearsall.

The following new members were elected: L. J. Rintoul, E. M. O. Laurie, L. J. Harris, I. H. Burkill, J. M. Lambert, F. A. L. Clowes, S. R. Nutman, G. R. Fenton, B. P. Urquhart and R. W. J. Keay.

Mr V. S. Summerhayes made a provisional statement on the financial position of the Society, saying that although publishing accounts had not yet been presented, he anticipated that with the generous aid of the Royal Society grant the year would end with a positive balance. On the proposal of Mr Summerhayes it was agreed that a grant of £10 be paid in 1943 to the Freshwater Biological Association. It was proposed by Prof. Osborn that Messrs William Norman and Sons be reappointed auditors, and this was agreed. On Dr Clapham's proposal the thanks of the meeting were unanimously given to the two Hon. Treasurers for their arduous and effective activities.

The report of the Hon. Secretaries on the work of the Society in 1942 was read and accepted in the form already approved by the Council.

Report of the Hon. Secretaries for the year 1942

The twenty-eighth Annual Meeting of the Society was held in the University Department of Botany, Oxford, on 3–5 January 1942. On the first evening Prof. and Mrs Osborn had provided an extremely pleasant social gathering in the Department, at which about 50 members and guests were present. During the evening Prof. Champion gave an illustrated lecture upon biotic influences on vegetation in the temperate Himalayas. On the following morning the meeting opened with Mr C. Diver's presidential

address on 'The Limits of Tolerance'. This was followed by the Business Meeting. In the afternoon there was a very pleasant excursion to Bagley Wood, under the leadership of Dr E. W. Jones, and in the evening the meeting was resumed in the Botanical Department, where there was shown an interesting series of exhibits illustrating different aspects of plant and animal ecology. During the evening several short talks were given explanatory of the exhibits. On Monday, 5 January, interesting ecological papers were read and discussed, the meeting closing at 4.30 p.m. The very sincere thanks of the Society are due to Prof. and Mrs Osborn, and to their colleagues, who made the meeting so outstandingly successful.

It was again discovered with regret that a summer excursion could not be arranged, members being unwilling or unable to attend such a meeting, though prepared to come to the Annual Winter meeting. To compensate in part for this a one-day meeting of the Society was held in London on 28 July to discuss the biological effects of the wartime ploughing-up policy. Papers were given by Prof. Sir R. G. Stapledon, Mr A. T. Roebuck, Dr A. C. Evans and Mr M. Graham, and a very considerable interchange of data on plant and animal ecology was achieved. This meeting, together with meetings of the Council, have been held in the rooms of the Linnean Society of London, to which body we are happy to express gratitude for hospitality thus provided.

Wartime printing difficulties have delayed the publication, and reduced the size of the journals. Nevertheless, two numbers of the *Journal of Ecology* have appeared, containing respectively 246 and 150 pages. Eleven original papers were published, with 27 plates, most of these illustrating a Burtt Memorial Supplement on East African Vegetation Communities, subsidized by the friends of our late members Mr B. D. Burtt and Mr C. F. M. Swynnerton. In addition, were published reviews, and parts of the Biological Flora on *Cladium mariscus*, the genus *Zostera* and *Aster Tripolium*. Within a few days the second part of vol. **12** of the *Journal of Animal Ecology* will have appeared, making a volume of 304 pages. The volume will then contain 17 original articles with 7 plates, together with reviews, and the usual comprehensive list of notices of publications on the Animal Ecology of the British Isles.

The accounts already published in the Biological Flora now number 10, several more are in the hands of the editorial committee, and there is a long list of members who have undertaken preparation of further accounts. The help of the Society has again been given to the Biology War Committee, this time in relation to inquiries as to the distribution of walnut trees. In view of the interest in National Post-war Reconstruction, the Council has appointed a committee to consider the question of Nature Reserves and National Parks from an ecological standpoint, and members have been asked to send information to the convener, Mr L. A. Harvey.

During the year the membership of the Society has risen from 363 to 378 members, 7 members having resigned or died, and 22 new members having been elected. Of the present membership list, 203 receive the *Journal of Ecology* alone, 122 the *Journal of Animal Ecology* alone, 51 take both journals, and 2 neither. It is extremely gratifying that our membership and attendance at meetings can be thus maintained.

The President reported the reduction in size of the journals imposed by paper shortage, and said that nevertheless there was a shortage of suitable papers for the *Journal of Ecology*. Mr Elton reported the Council's decision to print the *Journal of Animal Ecology* in smaller type, and Prof. Tansley, recalling his experiences during and just after the last war, urged all members who could do so, to contribute to the *Journal of Ecology* any papers worth publication.

The President apologized for failure of the Council to circulate names of nominees before the meeting: this was condoned, and the meeting unanimously elected the Council's nominees, as follows:

Hon. Secretaries: Dr H. GODWIN, Mr L. A. HARVEY.
Hon. Editor Journal of Ecology: Prof. W. H. PEARSALL.
Hon. Editor Journal of Animal Ecology: Mr C. S. ELTON.

Dr A. R. Clapham briefly reported on behalf of the Editorial Committee that 10 accounts of the Biological Fora had been published, 4 were ready for press, 5 nearly ready, and 56 promised, a total of 75. It was stated that with the help of a special taxonomic committee a memorandum on taxonomy and nomenclature had been prepared and accepted by Council for issue as a guide to procedure in the compilation of accounts. The President thanked the Editorial Committee and all who had helped in forwarding the publication of the Flora. In reply to Mr Wilmott, who raised the question of discrepancy between nominal and actual date of issue of the *Journal of Ecology*, it was stated that the Council had already taken steps to rectify the matter.

Dr Clapham then took the chair and Dr H. Godwin delivered his Presidential Address on 'Coastal peat-beds of the British Isles and North Sea'.

After the address the President resumed the chair and called on Dr K. B. Blackburn, who gave an account of the discovery of an elk skeleton (*Alces alces*) in a site at Neasham, near Darlington. The site had once been covered by the Stainmore Ice, but subsequently was occupied by a pool or lake, in which aquatic plants left very abundant fruits. The pollen diagram showed the elk to have lived in a birch-pine period prior to the extension of alder and oak, thus probably being late glacial or early post-glacial. In the following discussion Dr A. R. Clapham, Mr C. Elton, Dr H. Godwin, Mrs M. Bulman and Mr A. J. Wilmott took part.

After the adjournment for lunch Dr C. B. Williams gave a paper on 'The relation between numbers of individuals and numbers of species in random samples of fixed populations'. Data obtained in identified catches of insects in light traps were expressed in curves of number of individuals against number of species. The curves were shown not to be hyperbolic, but to conform to a series suggested by Dr R. A. Fisher:

$$n_1, \quad \frac{n_1}{2}x, \quad \frac{n_1}{3}x^2, \quad \ldots, \quad \frac{n_1'}{n}x^{n-1},$$

where x is less than unity. If the sums of the species and of individuals are known, this allows prediction of distribution of the population. The formula can be used to determine an 'Index of Diversity' of a population, and it was shown that it also fits some surprising sets of data, such as distribution of lice on human heads, and data of the type given by Willis on size of genera and species. In the discussion Dr A. R. Clapham, Mr G. E. Blackman, Mr C. Elton and Mr Kotval took part.

In 'Bracken: the frond and the plant', a further contribution to the ecology of bracken in Breckland was given by Dr A. S. Watt. An analysis was made of the factors influencing the height of the frond as it changes across the 'wave of advance' of bracken upon grass-heath. From the short outpost fronds there is a rise in height to a maximum followed, in some places, by no appreciable fall, in others by a fall to a fairly uniform short front in the hinterland behind the wave. The change in height was correlated with four factors: position of the frond on the plant, the age of the short shoot carrying the frond, the size of the bracken plant, and the depth of soil occupied by the rhizome. The initial rise in height is correlated with position on the plant—a phenomenon familiar enough in the upright plant—and at any one position on the plant there is a fall in height with age of the short shoot. A further fall in the height is related to the progressive reduction in size of the bracken plants from the invading margin backwards to the hinterland. On various soils the height of the frond is related to the depth to which the rhizome penetrates, and where the rhizome penetrates to about 40 in. there is only a slight fall from the region of maximum height. Thus the behaviour of the frond reflects the suitability of the habitat to bracken. The phenomena described for bracken are of widespread occurrence in species spreading vegetatively by rhizomes, and it was suggested that the phenomenon of the ageing of pastures was explicable, at least in part, on the basis of the findings for bracken. The President thanked Dr Watt for his paper, and called on Mr T. G. Tutin, who then gave his paper on the ecology of *Juniperus communis*.

Mr Tutin was concerned especially with the juniper in the north of England. It is a species occurring on very diverse soil types, from chalk and sand, to limestone pavement, slate, and *Sphagnum* peat bog, and it may have totally different associates in different habitats. Preliminary comparison of plants from the southern chalk and from the north of England slates shows that the latter have shorter, broader and more appressed leaves, but the significance of this is still obscure. In the north, juniper increases with diminution of grazing, and occurs with *Calluna* in the sere leading to oakwood. On northern limestones it takes part in the sere leading to ash-birchwood. Prof. Tansley, Mr Wilmott and Mr H. Gilbert-Carter spoke in the subsequent discussion.

After the President had thanked Prof. Brooks for the hospitality of his department the meeting concluded shortly after 4 p.m.

LIST OF MEMBERS (1 FEBRUARY 1943)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, Dr H. GODWIN, Botany School, Cambridge.

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E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
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THE INFLUENCE OF THE MINERAL COMPOSITION OF THE MEDIUM ON THE GROWTH OF PLANKTONIC ALGAE

PART II. THE INFLUENCE OF THE CONCENTRATION OF INORGANIC NITROGEN AND PHOSPHATE PHOSPHORUS

By S. P. CHU, *Department of Botany, Queen Mary College, University of London*

(*With fifteen Figures in the Text*)

I. THE INFLUENCE OF NITROGEN CONCENTRATION

Investigations of phytoplankton, in relation to the chemical composition of the sea and of various fresh waters, during the last twenty years show that phytoplankton is an important consumer of nitrogen and that its amount is often markedly affected by increase or decrease of the nitrogen content of the water. Exact relations between plankton growth and the amount of inorganic nitrogen have, however, not yet been precisely determined.

Among higher plants the rate of development is proportional to the uptake of nitrogen, and the latter is in turn dependent on the nitrogen concentration in the medium (Crowther, 1935; Miller, 1938, p. 643). A similar relation has been suggested in limnological studies by the fact that larger amounts of phytoplankton are often obtained in waters with a higher nitrogen content (Whipple, 1927, p. 213). Ketchum (1939), however, experimenting with the marine diatom *Nitzschia closterium*, has shown that the rate of division is independent of nitrate concentration. On the other hand, deficiency in nitrogen is usually considered to be one of the most important limiting factors in plankton production. It has also been claimed that nitrogen in solution may be concentrated to the point of injury (Welch, 1935, p. 186). There is, however, no general agreement on these matters. Wiebe (1930, pp. 141 and 169), investigating the plankton production in fish ponds, concludes that inorganic nitrogen is not a limiting factor, and a similar conclusion is reached in his investigation on the dissolved phosphorus and inorganic nitrogen in the water of the Mississippi (1931, p. 652). The following problems, therefore, await solution: (*a*) whether the nitrogen concentration in natural waters is commonly a limiting factor, (*b*) to what extent and at what concentration the growth of phytoplankton is limited by it, (*c*) whether higher concentrations are harmful and what are the injurious concentrations, and (*d*) within what limits an increase beneficially affects the development of phytoplankton, and within what limits the latter is indifferent to increase or decrease of nitrogen concentration.

Certain algae are found in waters with a low nitrogen concentration and others in waters with a higher concentration, while still others are met with both in low and high concentrations. Thus, Pearsall (1932) found that diatoms flourished when the water was richest in nitrates and that the appearance of *Asterionella* was correlated with higher concentrations than those occurring when *Tabellaria fenestrata* and green algae were found; further, that desmids occurred in summer when nitrates were low, while colonial

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green algae seemed to require higher concentrations of nitrates than desmids. It has not, however, been established experimentally that such differences in nitrogen requirements actually exist between different planktons, and it remains possible that the relations found are coincidences. It is of interest, therefore, to determine precisely how varying concentrations of nitrogen affect the growth of different phytoplankton organisms.

Nitrate nitrogen is generally considered to be more readily available to plants than ammoniacal nitrogen, although several investigations show that certain plants grow equally well whether the source of nitrogen be an ammonium salt or a nitrate, while some show better growth with ammonium salts (Allison, 1931; Miller, 1938, p. 644). The relative value of these two forms of nitrogen thus differs in different plants. The ability of certain algae to utilize ammonium nitrogen has already been demonstrated by Treboux (1904), Pringsheim (1912), Schreiber (1927), Braarud & Föyn (1930), Pearsall & Loose (1937), and Harvey (1940). Exps. 5, 6, 9, 10 and 12–17, described in the first part of this paper (Chu, 1942), also show growth of the algae studied when ammonium salts are supplied as the source of nitrogen. Both forms of nitrogen occur in natural waters, although the larger part of that present in the surface layers is often in the form of nitrates. Whipple (1927, p. 298) concluded that the nutritional value of ammoniacal nitrogen to aquatic organisms lies in the 'potential, rather than immediate, ability to develop plant life', and that 'high ammonia nitrogen in stream waters does not often afford certain evidence of an abundance of such organisms'. It is therefore also of importance to ascertain whether ammonium nitrogen can be directly utilized by freshwater planktonic algae, and, if so, whether the relative value of ammonium salts and nitrates varies as among higher plants.

Observations on the occurrence of organisms in their natural habitats often provides very suggestive and useful data, and conclusions drawn from these are frequently likely to be correct, but, in view of the complex interrelations of physical, chemical and biological factors, such conclusions cannot be regarded as entirely reliable. They may indeed often prove to be only partially correct or even altogether erroneous. The experiments described below were undertaken under known controlled conditions with a view to determining the relation between the development of planktonic algae and the nitrogen concentration of the medium, whether supplied as ammonium or nitrate.

(*a*) **Pediastrum boryanum** (Turp.) Menegh.

Exp. 2, described in the first part of this paper (Chu, 1942, p. 301), shows a marked difference in the growth of *Pediastrum* in solutions with different amounts of NH_4NO_3. The effect of different concentrations of nitrogen was further examined by using various media that have proved to be suitable for the growth of this alga.

Exp. 18. Medium 5 (Chu, 1942, p. 298), with $(NH_4)_2SO_4$ (1) 0·1, (2) 0·5, (3) 1·0, (4) 5·0, (5) 10, (6) 25, (7) 50 and (8) 100 p.p.m. (N = 0·02, 0·11, 0·21, 1·06, 2·1, 5·3, 10·6 and 21·2 p.p.m.) in quadruplicate sets of 50 c.c. cultures (series A). Since in series A there is also a change in SO_4 concentrations, a parallel series (B) with medium 6 was undertaken; here NH_4Cl is the source of nitrogen, the amounts supplied varying from 0·1 to 100 p.p.m. [N = (1) 0·03, (2) 0·13, (3) 0·26, (4) 1·3, (5) 2·6, (6) 6·5, (7) 13·1 and (8) 26·2 p.p.m.], again in quadruplicate 50 c.c. cultures. Cultures of both series inoculated from a young subculture in medium 5, so that at the beginning there were approximately 100 colonies per c.c. of the solution. Cultures exposed in illuminating apparatus C (Chu, 1942, p. 286), two of each concentration of the respective series for 7 hr. daily, the remaining two for 16 hr. daily. The growth in the different sets of cultures corresponded very well, except that cultures 4–8 in both series provided with longer illumination developed more quickly especially during the first few days; there was no noticeable difference in cultures 1–3 which were very poor. The growth of one set of cultures from either series with 7 hr. daily illumination is plotted against the actual nitrogen concentration in Fig. 9, from which the marked correspondence of the two series is evident.

Two further sets of cultures, using media 5 and 6 respectively, were undertaken with the same gradations of concentrations of ammonium salts, but without any phosphate, one set being exposed to continuous illumination and the other 7 hr. daily in apparatus C. There was hardly any growth in any of the cultures, evidently because of lack of phosphate. Weekly analyses for ammonium (direct nesslerization) and nitrate (phenoldisulphonic acid method) showed that no noticeable nitrification was taking place in any culture. The capacity of the alga to absorb nitrogen from ammonium, as demonstrated in Exp. 5 (Chu, 1942, p. 305), is therefore further confirmed. Similar results were obtained in Exps. 19, 21, and 23–25 using duplicate sets of cultures without phosphate. The different growth in cultures supplied with different amounts of $(NH_4)_2SO_4$ or NH_4Cl, dealt with below, must be due to the varying concentration of ammoniacal nitrogen.

In series A appreciable multiplication had occurred after 6 days in cultures 5–8 (Fig. 9, *A*), the growth in the last culture being slightly inferior to that in 5–7; there was a slight increase in culture 4, but in 1–3 the growth was very poor and the difference between them insignificant. The number of colonies in cultures 1 and 2 after 12 days was only twice that when the cultures were started and there was no subsequent increase. On the other hand, there was pronounced multiplication in cultures 5–8 during the second 6 days (Fig. 9, *AA*), as compared with the very slight increase in 3 and 4, and at the end of 19 days the difference was still more marked.

In series B (Fig. 9, *B*, *BB*) cultures 4–8 showed good growth during the first 5 days, but 10 days later the increase in 4 was much inferior to that in 5–8. 5 p.p.m. of NH_4Cl therefore provides a nitrogen concentration (1·3 p.p.m.) sufficient for the multiplication of about 100 colonies per c.c. for at least 5 days, and this amount of nitrogen is sufficient to support the development of about 1650 colonies with an average diameter of 42 μ, without any indication of nitrogen deficiency. At some time after the sixth day, however, the nitrogen content falls to a level below which multiplication can no longer keep pace with that in cultures with a higher nitrogen concentration. The growth in cultures 1–3 of series B corresponds to that in series A, but that in culture 4 of B is definitely better than in culture 4 of A, which must be due to the higher nitrogen content of corresponding cultures of series B. At the end of 19 days the most abundant growth was in culture 7 of this series (N = 13·1 p.p.m.). That in culture 8 (N = 26·2 p.p.m.) was inferior to that in 7 during the whole period of the experiment (19 days). There seemed to be a slight inhibiting effect due to the high nitrogen concentration in this last culture.

Growth is thus very small or negligible in solutions with a nitrogen concentration of 0·11 p.p.m. or less, and is still insignificant with nitrogen at 1·06 p.p.m., which is a very common nitrogen concentration in natural waters (Chu, 1942, Table 7). Above this point the rate of multiplication steadily increases with increased nitrogen concentration for the first 5 or 6 days (Fig. 9, *A*, *B*), up to an optimum which ranges from 1·3 to 13·1 p.p.m.

A week later, as the nitrogen falls below the lower optimum limit of 1·3 p.p.m., the growth in culture 4 becomes less and less vigorous, and the best growth now occurs in cultures with an original nitrogen concentration of 2·1 p.p.m. upwards. This progressive shift of the cultures giving the best growth proceeds until the 19th day, when only that with an original nitrogen concentration of 10·6 to 13·1 p.p.m. shows optimum growth. Such changes, resulting from a progressive depletion of nitrogen, are also observed in the culture series of Exps. 19 and 20.

The nitrogen concentration also affects the distribution of *Pediastrum* in the fluid. The colonies usually sediment as soon as the nitrogen concentration decreases to a level below that most suitable for multiplication; for example, most of the larger colonies sedimented 12 days after inoculation in culture 4 of series B, while 3 days later sedimentation set in in culture 5 at a time when the colonies in 6–8 were still evenly distributed; 4 days later sedimentation commenced also in these.

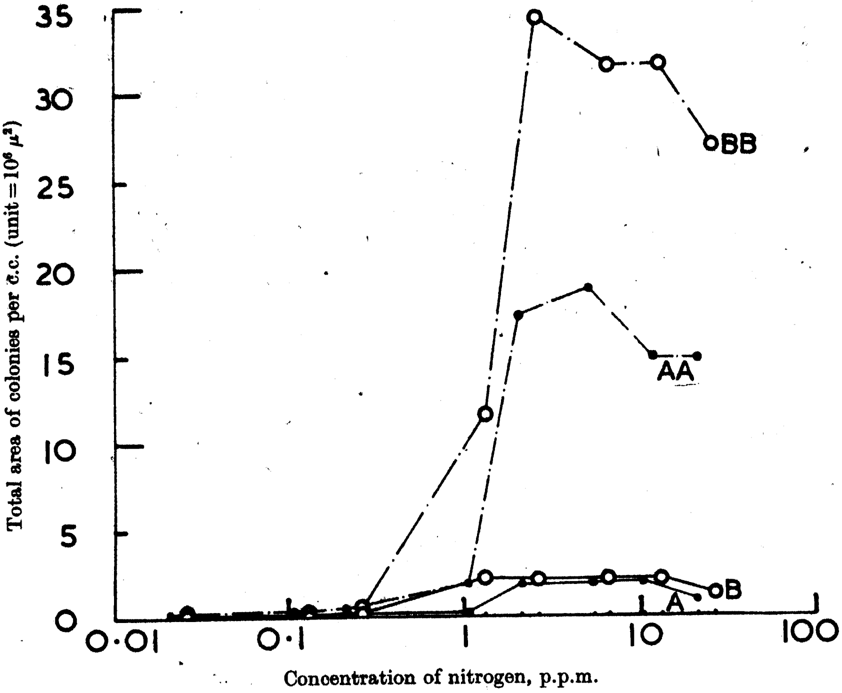

Fig. 9. Growth of *Pediastrum boryanum* in different concentrations of ammoniacal nitrogen (Exp. 18, media 5 and 6): *A*, 6 days and *AA*, 12 days of series A; *B*, 5 days and *BB*, 15 days of series B.

In cultures showing such sedimentation the cells of the colonies exhibit an increased size and the accumulation of abundant reserve material so that sinking may possibly be due to an increase in weight. The protoplasts in such sedimenting colonies often exhibit more or less complete cleavage, but the products of division are not differentiated and the young colonies are not liberated. The phenomenon of sedimentation seems to be mainly due to retardation or suppression of multiplication as a result of unfavourable conditions, caused by the depletion of nitrogen in the culture. Similar phenomena were observed in Exps. 19 and 20. In nature such sedimentation of *Pediastrum* colonies, as a result of nitrogen deficiency, might be beneficial in waters with a higher nitrogen concentration at lower levels, where normal multiplication might be resumed.

Sedimentation is also facilitated by clustering of the colonies, the daughter colonies tending to cling together by the mucilaginous tips of the projections of the peripheral cells. This is often, but not always, observed in the sedimented cultures.

Pediastrum retains its vitality for a certain period in cultures deficient in nitrogen. 1·25 mg. of $(NH_4)_2SO_4$ was added to each of cultures 1–4 of series A, and a similar amount of NH_4Cl to cultures 1–3 of series B, 19 days after inoculation when the colonies had assumed a white appearance. One month after such treatment all these cultures exhibited a very luxuriant growth.

In cultures with suitable nitrogen concentrations the size of the coenobia and the number of constituent cells tend to increase with the nitrogen concentration. The inocula introduced into all the cultures of both series were derived from the same culture which was well shaken so that the colonies were evenly distributed. The variation in size and number of constituent cells was not therefore due to differences in the inocula. This is further confirmed by the following experiment, where the inocula for all the cultures comprised the same numbers of colonies of the same size and with the same number of constituent cells.

Table 23

Cultures		$(NH_4)_2SO_4$ (series A), NH_4Cl (series B), p.p.m.	16 days		
			Average size of coenobia μ^2	Total area per c.c. × $10^5\mu^2$	Average no. of constituent cells of the coenobia
Series A:	4	5	1397	24·0	25·3
	5	10	1645	51·3	27·0
	6	25	1956	53·5	30·7
	7	50	2699	52·0	41·3
	8	100	1126	42·0	18·8
Series B:	4	5	1525	42·8	22·5
	5	10	1755	52·8	27·8
	6	25	1776	53·2	28·6
	7	50	3880	52·0	32·5
	8	100	2530	40·4	32·0

Exp. 19. This was practically a repetition of Exp. 18 in which particular care was taken to ensure uniformity of the inocula. Twenty selected 32-celled coenobia from a young culture in medium 6, each 74 μ in diameter, were inoculated into media 5 (series A) and 6 (series B) with the same gradations in the nitrogen-containing salts as in Exp. 18. They were illuminated in apparatus C for 7 hr. daily.

The results were comparable to those of Exp. 18, growth being exceedingly poor in cultures 1–3 of both series throughout the experiment. The best growth during the first 12 days was in cultures 5–7 of series A and in cultures 4–7 of series B. Four days later the growth in culture 4 of B was a little inferior to that in 5–7 which showed no notable differences in the amount of growth; this was still so after another 6 days. Culture 8 in both series was the second best during the whole period of the experiment (22 days). The shift of optimum growth to higher nitrogen concentrations took place more slowly than in Exp. 18, no doubt because the amount of inoculum is much smaller in Exp. 19.

Table 23 shows the results after 16 days' growth in one set of each series. As in the cultures of Exp. 18, the average size of the coenobia and the average number of their constituent cells increase with increasing concentration of the nitrogen-containing salts up to 50 p.p.m. in both series, notwithstanding the fact that the original inocula consisted of uniform coenobia. The percentage of 8-celled coenobia decreases and that of 64-celled coenobia increases with increasing nitrogen concentration within this range. There seems again to be a slight unfavourable influence in culture 8 of both series with the highest nitrogen concentration; in this culture the size of the coenobia decreased, and the average number of constituent cells, though still large in series B, showed a decrease in series A.

Exp. 20. Since both in Exps. 18 and 19 there were indications of an unfavourable effect of the highest nitrogen concentrations used, it was decided to investigate the effects of still higher concentrations. In this experiment medium 8 with KNO_3 as the source of nitrogen was used, the amount varying from 0 to 500 p.p.m. with nitrogen concentrations of (1) 0, (2) 0·014, (3) 0·14, (4) 0·69, (5) 1·39, (6) 3·46, (7) 6·93, (8) 10·4, (9) 13·9 and (10) 69·3 p.p.m.; duplicate series of ten cultures were prepared in large tubes holding 40 c.c. (series A) and 50 c.c. (series B) respectively of the medium; inoculum approximately twenty-five colonies (mostly 16- and 32-celled, with an average area of 1600 μ^2) per c.c. from a young culture in medium 8; series A exposed to continuous illumination (apparatus C) at a temperature of 17·5 ± 0·5° C., B for 7 hr. daily at a temperature of 22 ± 2° C. The average growth of the duplicate sets of cultures of each series in different nitrogen concentrations expressed as turbidity estimated at different periods is shown in Fig. 10.

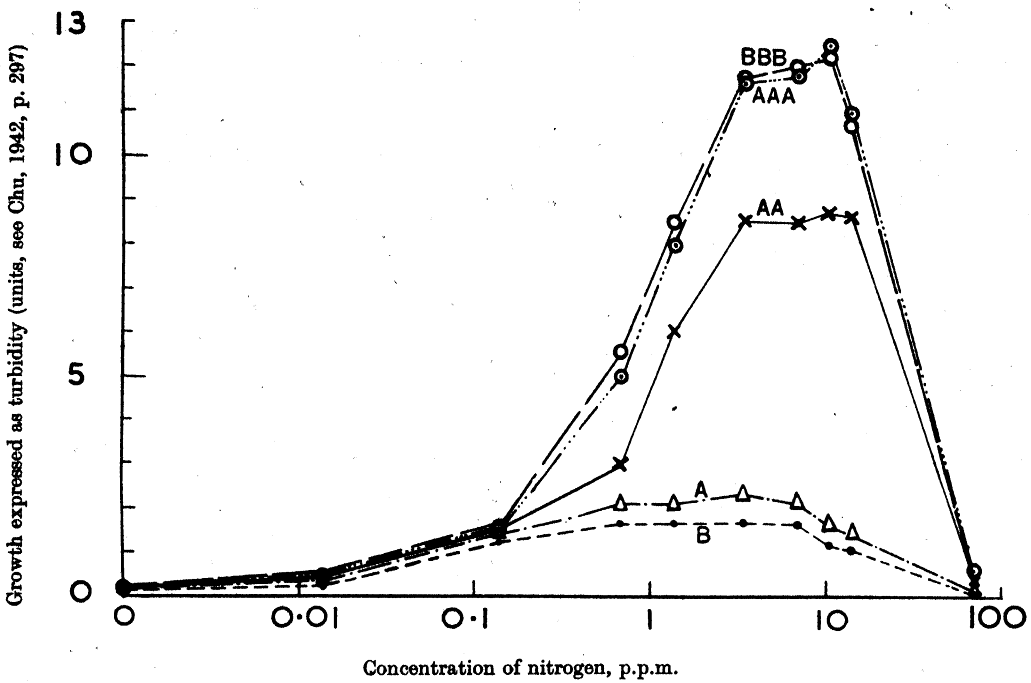

Fig. 10. Growth of *Pediastrum Boryanum* (average of duplicate sets) in different concentrations of nitrate nitrogen in medium 8 (Exp. 20): *A*, *AA*, and *AAA*, 14, 35 and 86 days' growth respectively of series A; *B* and *BBB*, 13 and 86 days' growth respectively of series B.

The growth in the different sets of cultures of the two series corresponds closely, although that of series A with continuous illumination was noticeably better, especially during the first fortnight, apart from cultures 1, 2 and 10 which showed equally poor growth with both periods of illumination; after the first fortnight the difference became less and less pronounced. The growth in series A never reached twice that in the corresponding cultures of series B, though series A was illuminated for more than three times the daily period of illumination of B.

The shifting of optimum growth from lower to higher nitrogen concentrations, as the experiment proceeded, took place as in the previous experiments, the best growth being first observed in cultures 4–7, then in 5–9 and finally in 6–9. The cultures in the lower concentrations soon became paler and less green; 3–6 changed from green to yellowish in 45 days in series B and were nearly white at the end of 86 days, at a time when cultures 7–9 were still green. The decrease in colour in cultures of series A occurred earlier than in cultures of series B. In the tenth culture of each series, with a nitrogen concentration of 69·3 p.p.m., there was a marked inhibiting effect throughout, the growth always remaining as poor as in cultures 1 and 2.

The lower limit of nitrogen concentration for optimum growth of *Pediastrum*, under the conditions of this experiment, is approximately 0·69 p.p.m. or possibly still lower as good growth was still obtained in a concentration of 0·14 p.p.m., though inferior to that obtained in 0·69 p.p.m. The upper limit seems to be round about 6·93 p.p.m., although the inhibiting effect in 13·9 p.p.m. is slight. Good growth can also be obtained in cultures with a nitrogen concentration up to 26 p.p.m., as shown in culture 8 of series B, Exps. 18 and 19, where the inhibiting effect was by no means serious.

In series A of Exps. 18 and 19 the growth in cultures with a nitrogen concentration of 1·06 p.p.m. was evidently below the optimum level, while in Exp. 20 optimum growth occurred in 0·69 p.p.m. The lower limit of the optimum range of nitrogen concentration for the growth of *Pediastrum* in medium 5 with $(NH_4)_2SO_4$ as a nitrogen source is therefore higher than that in medium 8 with KNO_3 as a nitrogen source. The growth in a nitrogen concentration of 0·14 p.p.m. in Exp. 20 was definitely better than in nitrogen concentrations from 0·13 to 0·26 p.p.m. in Exps. 18 and 19. It thus seems that, although *Pediastrum* can utilize nitrogen either in the form of nitrates or of ammonium salts, ammoniacal nitrogen below a certain concentration is less readily utilized than a similar concentration of nitrate nitrogen. Since inorganic nitrogen in natural waters is mostly in the form of nitrate, Exp. 20 probably gives a truer picture of what happens in nature than do Exps. 18 and 19. In cultures with a nitrogen concentration less than 0·1 p.p.m. the growth is always poor, no matter whether nitrate or ammonium salts are supplied.

In waters poor in nitrogen, such as the English lakes where the nitrogen concentration is seldom more than 0·2 p.p.m. and never reaches the lower optimum limit as established by these experiments, *P. boryanum* can only be scantily represented in the plankton. It is recorded only in the silted lakes, where there is more nitrogen (West & West, 1909; Pearsall & Pearsall, 1925; Wailes, 1939). In the river Wharfe, *Pediastrum* was found during June and July only in the Ulleskef region, with a nitrogen concentration of 0·9 p.p.m., which is higher than in other parts of the river; it was not present in subsequent months when the nitrogen concentration decreased (W. R. R. B. 1930, p. 285; Schroeder, 1930, p. 304). In the Illinois, where *Pediastrum* was always present (Kofoid, 1908, p. 26), the nitrogen content is never much below the lower optimum limit established by Exp. 20, and the *Pediastrum* pulses are stated to be related to the nitrate pulses. The occurrence of *Pediastrum* in natural waters therefore roughly corresponds with the conclusions derived from Exps. 18–20.

The average nitrogen concentration of the analyses of surface waters by the Metropolitan Water Board in 1937 was 2·96 p.p.m. If this can be considered as representing a usual condition in natural waters in southern England, a population of *Pediastrum* of about 20,000–35,000 colonies per c.c., with an average area of 1000 μ^2, might be expected to be present, if sunshine and other factors were suitable. This may be deduced from series A and B of Exp. 18. Even if 1·08* p.p.m., as estimated by Murray (1887), be taken as the average nitrogen concentration of river water, a similar growth might be expected, since Exp. 20 shows that, when nitrate is the source of nitrogen, about equal growth occurs in nitrogen concentrations of 0·69–3·46 p.p.m. or more. In nature, however, the quantity of *Pediastrum* is often much below this estimate. The pond sample from which the material was originally isolated, although it appeared to be unusually rich in *Pediastrum*, only contained 13,000 colonies per c.c. The relatively smaller number may be due to many causes, such as competition, inadequate illumination, unsuitable concentration of other dissolved substances and so on.

(*b*) **Staurastrum paradoxum** Meyen

Exp. 21. Media 5 (series A) and 6 (series B), with the nitrogen-containing salts varying from 0·1 to 100 p.p.m. in eight cultures (10 c.c.) as in Exp. 18; four sets for each series; illumination in apparatus C for 7 hr. daily; inoculum approximately 120 individuals per c.c. from a culture in medium 3.

The amount of growth in different nitrogen concentrations agrees well in the four sets of cultures of each series and remained similar during the whole period of the experiment (85 days). In series A good growth was obtained in cultures 5–8 (N = 2·1–21·2 p.p.m.), the best being in culture 6 with 25 p.p.m. of $(NH_4)_2SO_4$ (N = 5·3 p.p.m.), the second best in culture 5 and the third in cultures 7 and 8. In series B good growth was obtained in cultures 4–7 (N = 1·3–13·1 p.p.m.), the best being in culture 5 with 10 p.p.m. of NH_4Cl (N = 2·6 p.p.m.), the second best in cultures 4 and 6 and the third in culture 7. The growth in other cultures was very poor; the individuals, though remaining normal, divided only once or twice during a period of 37 days. Cultures with a nitrogen concentration from 2·1 p.p.m. (culture 5, series A) downwards showed the effects of nitrogen deficiency, while those with a nitrogen concentration from 6·54 p.p.m. (culture 6, series B) upwards showed an increasing inhibiting effect. The optimum concentration of ammoniacal nitrogen for the growth of *Staurastrum paradoxum* is therefore within the range 2·1–6·5 p.p.m. and probably near 5·3 p.p.m. This is the concentration provided in culture 6 of series A, which produced 11,100 cells per c.c. in 37 days. This supports better growth than culture 5 of series B (with 2·6 p.p.m. of nitrogen) which only gave 9250 cells per c.c. in 37 days. The suitable range of ammoniacal nitrogen is therefore much narrower for *S. paradoxum* than for *Pediastrum*, whose optimum growth occurred in nitrogen concentrations from 1·3 to

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* The average of surface water (Murray, 1887) in Table 7 (Chu, 1942, p. 304) was calculated using Clarke's (1924) percentage figures and Pearsall's (1922) figure 152 p.p.m. as the average total dissolved substances; whereas calculating directly from Murray's data using the shipping ton (1016·06 kg.) and English mile (1600·3 m.) as used by Murray, the averages obtained are: N = 1·08, P = 0·136, Fe = 2·22, Ca = 34·6, Mg = 7·93, K = 2·23, Na = 5·9, SiO_2 = 18·2, organic matter = 19·3 and total dissolved substances = 186 p.p.m. If 186 p.p.m. is taken as the average of dissolved substances, the averages from Clarke's data are: N = 0·38, Fe + Al = 4, Ca = 37·9, Mg = 6·3, K = 3·94, Na = 10·8, SiO_2 = 21·7 p.p.m.

6·5 p.p.m. and which can tolerate a nitrogen concentration of 26·2 p.p.m. (culture 8, series B, Exps. 18 and 19) which exerts a serious inhibiting effect on *Staurastrum paradoxum*, an effect which is still evident, though slightly lessened, in later stages of the experiment.

The growth in the cultures of series A is comparable to that in corresponding cultures of series B, except that cultures 4 and 5 in A showed a growth considerably inferior to that of cultures 4 and 5 in B, although the difference in nitrogen concentration is not very great. *S. paradoxum* exhibits a very slow growth rate in the media used. Even in optimum concentrations of nitrogen, only 5–7 divisions occurred in 37 days in either series. The growth in one set of cultures of series B during 37 and 75 days, expressed as number of cells per c.c. and turbidity respectively, is shown in Fig. 11, *A*, *B*.

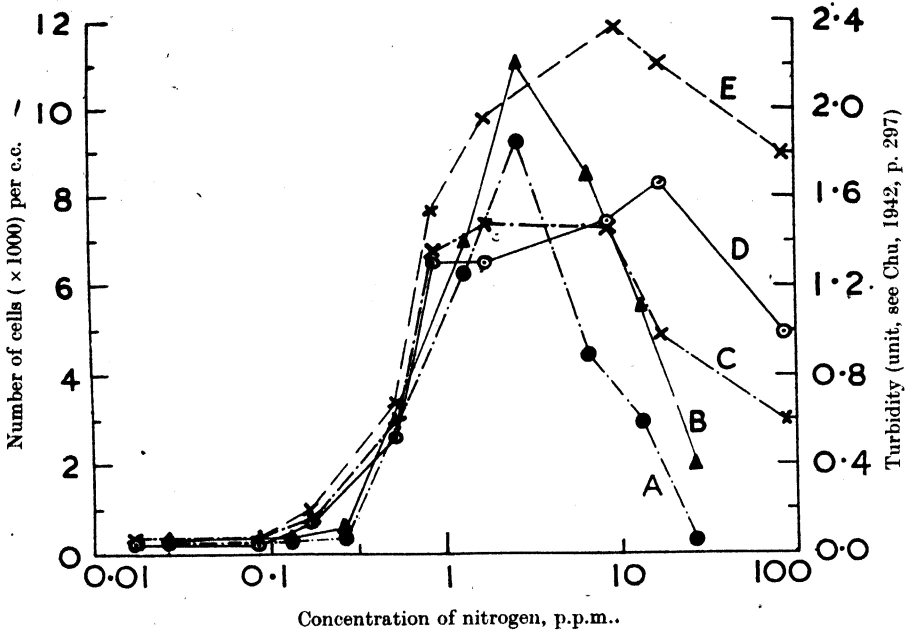


Fig. 11. Growth of *Staurastrum paradoxum* in different concentrations of ammoniacal (curves *A* and *B*, Exp. 21) and nitrate (curves *C*, *D* and *E*, Exp. 22) nitrogen: *A* (37 days, number of cells) and *B* (75 days, turbidity), series B, Exp. 21; *C* (turbidity) and *D* (number of cells), 32 days; *E* (turbidity), 69 days, Exp. 22.

Exps. 18–20 afforded evidence of a noticeable difference between the effect of lower concentrations of ammonium salts and of nitrates respectively on the growth of *Pediastrum*. The following experiment was carried out with the object of ascertaining whether a similar difference exists in the case of *Staurastrum paradoxum*.

Exp. 22. Medium 9 with $Ca(NO_3)_2$ (1) 0·1, (2) 0·5, (3) 1·0, (4) 3·0, (5) 5·0, (6) 10, (7) 50, (8) 100, and (9) 500 p.p.m. (N = 0·017, 0·085, 0·17, 0·51, 0·85, 1·7, 8·5, 17·1 and 85·4 p.p.m.); quadruplicate sets of nine 10 c.c. cultures with 7 hr. illumination daily in apparatus C; inoculum approximately 1800 individuals from a culture in medium 9. For the resulting growth in one set of cultures see Fig. 11, *C*, *D* (after 32 days) and Fig. 11, *E* (after 69 days).

The growth in the various sets of cultures agreed well. The difference between the growth in cultures with ammonium salts and those with nitrates is just as striking as for *Pediastrum*. The growth of *Staurastrum* in cultures with ammonium nitrogen not exceeding 0·26 p.p.m., as shown in Exp. 21 (Fig. 11, *A*, *B*), is very poor. When nitrogen is supplied as a nitrate, a concentration of 0·17 p.p.m. definitely supports better growth than does 0·26 p.p.m. of ammoniacal nitrogen (cf. Fig. 11, *A*, *B* and *C*, *D*), while the growth in concentrations of 0·51 and 0·85 p.p.m. is considerably superior to that in 1·06 p.p.m. of ammoniacal nitrogen in Exp. 21, series A.

The optimum growth in Exp. 22 occurred in nitrogen concentrations from 0·85 to 8·5 p.p.m., and there is no noticeable difference of growth in these concentrations during the first 4 weeks (5–6 cell divisions). A week or so later, however, the growth in cultures which originally contained 8·5 p.p.m. of nitrogen, exceeded that in the lower concentrations, in which consumption of nitrogen had presumably reduced the level to below the optimum range. The number of cells in culture 8 (N = 17·1 p.p.m.) was about the same as in cultures 5–7 (N = 0·85–8·5 p.p.m.) during the first 4 weeks, but subsequently the number became larger than in the other cultures. The size of the cells in culture 8 is, however, less and the processes are not so well developed, which may indicate an unfavourable effect of the higher nitrogen concentration. This may also explain the discrepancy between the different estimates obtained by counting and turbidity (cf. Fig. 11, *C*, *D*). A slight shortening of the processes in culture 7 was also noticeable. In the ninth culture, with a nitrogen concentration of 85·4 p.p.m., the processes were very short.

It is evident that *S. paradoxum* can tolerate relatively high concentrations of nitrate nitrogen much better than high concentrations of ammoniacal nitrogen; there is no inhibiting effect on the rate of reproduction in 17·1 p.p.m. of nitrate nitrogen, while this is appreciable in 6·5–13·1 p.p.m. of ammoniacal nitrogen (Exp. 21, Fig. 11, *A*, *B*). A definite inhibiting effect occurred only in the last culture of Exp. 22 (N = 85·4 p.p.m.), and even here there is still moderate growth, while the effect is diminished as the nitrogen concentration decreases. With ammoniacal nitrogen a concentration of 26·2 p.p.m. (Exp. 21, culture 8, B) already exerts a serious inhibiting effect. *S. paradoxum* can tolerate higher concentrations of nitrate nitrogen rather better than *Pediastrum* (cf. Fig. 11, *C*, *D* and *E*, with Fig. 10), although the latter has a higher degree of tolerance towards ammoniacal nitrogen (cf. Fig. 11, *A*, *B*, with Fig. 9).

Exp. 22 admits of the following conclusions. There is scarcely any growth of *Staurastrum paradoxum* in media with a nitrogen concentration of 0·085 p.p.m. or less, but above that point the amount of growth increases with increasing nitrogen concentration and under suitable conditions optimum growth is possible with concentrations from 0·85 p.p.m. upwards. No inhibiting effect owing to high nitrogen concentrations is likely in natural waters in which the nitrogen concentration rarely exceeds 8·5 p.p.m. If other conditions are suitable for growth, it will only be when the nitrogen concentration remains above 0·85 that the development of this desmid in natural waters will be unaffected by alterations in the nitrogen content of the water; below that limit its multiplication should be markedly affected by a rise or fall of the nitrogen content.

It is only in Ennerdale in the Lake District that the concentration of nitrate nitrogen normally remains below 0·08 p.p.m. (Pearsall, 1930, p. 318; 1932, appendix) and *S. paradoxum* is not recorded from it. Of the lakes in which this desmid is found, Crummock Water alone has a nitrate nitrogen concentration which does not usually exceed 0·09 p.p.m.; in the others the upper limit of nitrogen concentration varies between 0·1 and 0·2 p.p.m., although it never reaches the concentration necessary for optimum growth. This is no doubt one of the reasons why this desmid never occurs here in great abundance, although phosphate deficiency is probably another limiting factor. It is of interest to compare the frequency of *S. paradoxum* with the nitrogen content in the various lakes (Table 24). The correspondence between the increasing concentration of nitrogen on the one hand, and the increasing percentage of *S. paradoxum* on the other, can hardly be accidental.

Table 24. *Occurrence of* Staurastrum paradoxum *in relation to the concentration of nitrate nitrogen (p.p.m.) in the English lakes (based on Pearsall's data,* 1930, 1932)

Lakes	% of *S. paradoxum*	N concentration
Crummock	1	0·024–0·09
Esthwaite	1	0·013–0·17
Lowes Water	2	0·022–0·12
Bassenthwaite	3	0·030–0·16
Windermere	5	0·048–0·20

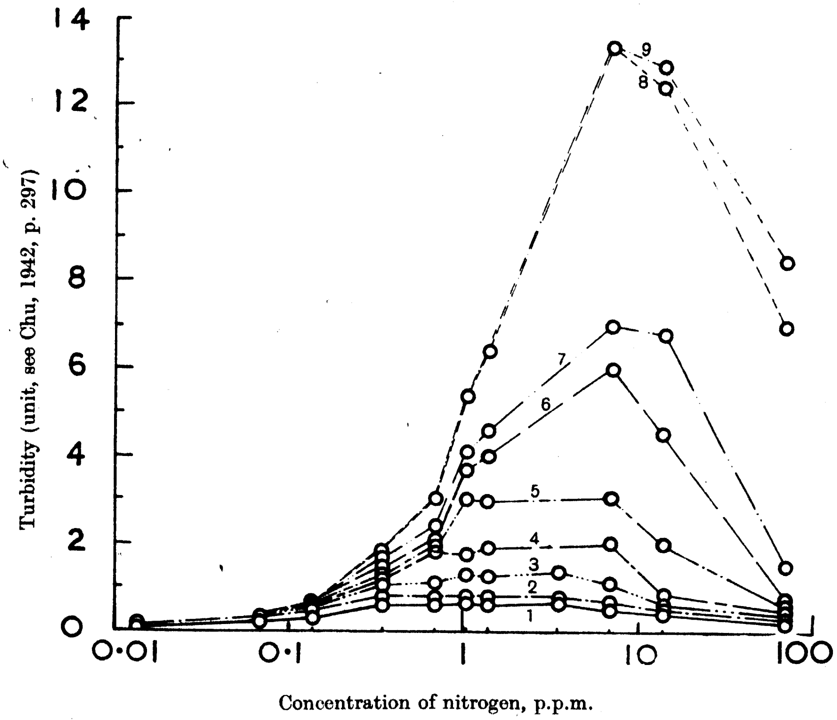


Fig. 12. Growth of *Botryococcus Braunii* in different concentrations of nitrate nitrogen, expressed as turbidity: (1) 13, (2) 33, (3) 44, (4) 53, (5) 64, (6) 73, (7) 106, (8) 187 and (9) 232 days; Exp. 23, medium 13.

(*c*) **Botryococcus Braunii** Kütz.

Exp. 23. Medium 13, duplicate series of eleven 50 c.c. cultures with KNO_3 (1) 0·1, (2) 0·5, (3) 1·0, (4) 2·5, (5) 5·0, (6) 7·5, (7) 10, (8) 25, (9) 50, (10) 100 and (11) 500 p.p.m. (N = 0·014, 0·069, 0·139, 0·346, 0·69, 1·04, 1·39, 3·46, 6·93, 13·9 and 69·3 p.p.m.); illuminated 17 hr. daily in apparatus C; inoculum 4 drops from a culture in medium 13, each drop containing on the average 170 colonies, 20–55 μ in diameter. The growth at various periods in different nitrogen concentrations of one series, expressed as turbidity, and plotted against the concentration of nitrogen, is shown in Fig. 12.

The duplicate cultures showed good correspondence. The lower limit of nitrogen concentration for an optimum growth of *Botryococcus* is about 0·35 p.p.m. (Fig. 12, 1, 2), since no noticeably better growth is obtained in higher concentrations during the first 5 weeks, while in lower concentrations the growth is progressively less. There was very little growth in the first culture. The upper optimum limit seems to be about 6·9 p.p.m. or a little less (Fig. 12, 1–3), since a slight inhibiting influence is at first observed in this concentration, although after 7 weeks the growth was not inferior to that in other concentrations and after about 10 weeks this culture showed the best growth of all. The range of optimum nitrogen concentration is therefore approximately from 0·35 to nearly 6·9 p.p.m.

In later periods the optimum growth changed in the usual way to cultures with higher initial nitrogen concentrations; after 7 weeks optimum growth occurred in cultures 5–9 and after 15 weeks in 9 and 10. The inhibiting effect in concentrations of 6·9 p.p.m. and upwards, observed during the first 7 weeks, gradually decreased later, although in culture 11 (N = 69·3 p.p.m.) it was still considerable at the end of 34 weeks. Such a nitrogen concentration is, however, far less deleterious for *Botryococcus* than for *Pediastrum* (cf. Fig. 10, Exp. 20). Even in the early stages of the experiment *Botryococcus* grew slowly but steadily in this high concentration, and after a year this last culture was the only thriving one in the series, containing large deep green colonies at a time when all the others had successively become yellowish and then almost white.

Very few natural waters have an average concentration of nitrogen below that in culture 1, and in many the lower limit for the optimum growth of *Botryococcus* is surpassed (cf. Chu, 1942, Table 7). Its widespread occurrence and the not uncommon formation of water-flowers is therefore comprehensible, although deficiency in phosphate, or harmful excess of Mg, K, or SiO_2 (Exp. 13, Chu, 1942, p. 315), probably often affect its abundance. *Botryococcus* has been reported in Ennerdale, Crummock Water, Derwentwater, Windermere and Ullswater (Pearsall, 1932, appendix; West & West, 1909, p. 140), with nitrate nitrogen varying from 0·048 to 0·124 p.p.m., although it never occurs in considerable quantities. This is to be expected, since the nitrogen concentration is far below the lower limit for optimum growth and growth is further restricted by the deficiency in phosphate.

The change of colour in the cultures is noteworthy. The colonies, which are green at first, become yellowish green, then yellowish and finally opaque and whitish brown, as the nitrogen in the solution is gradually used up. This change proceeds progressively from cultures 1–9 in both series. The first three cultures became whitish brown after 15 weeks, at a time when 4 and 5 were yellowish green and the remainder green, the depth of the green colour in cultures 6–11 increasing with the nitrogen concentration. This indicates that, as in higher plants, more nitrogen is taken up by the alga in higher nitrogen concentrations, and that the amount of nitrogen absorbed affects the formation of chlorophyll.

There are also distinct morphological differences among the *Botryococcus* colonies, supplied with different amounts of nitrogen. The most striking are as follows:

(1) In cultures (e.g. no. 1) with a very low nitrogen concentration the colonies are very small, while they increase in size with increasing nitrogen concentration, until the upper limit of the experiment is reached.

(2) In higher nitrogen concentrations the parietal chromatophore is thicker and more

extensive, the mucilage envelope is firmer and more viscous, and the cells are more compactly arranged; in lower concentrations they are fewer and more widely spaced.

(3) In higher nitrogen concentrations the cells are larger and longer in proportion to their width, while their inner extremities are narrower and usually more definitely prolonged into a stalk-like process. Thus, in culture 3 after 6 months the cells are 6·5–7·6 μ long and 4·3–5·4 μ wide, while in culture 11 they are 7·6–12 μ long and 3·2–5·4 μ wide.

(4) There is no marked difference in the actual production of oil by the colonies in cultures with different nitrogen concentrations, but the proportion of oil to the number of cells within the colony is larger in the lower concentrations.

In nature *Botryococcus* occurs as large green colonies or as small brownish ones; there are also intermediate grades. Although no detailed chemical data are available, it seems probable that *Botryococcus* occurs as small brown colonies in waters deficient in nitrogen. According to Gams (1923) Swiss waters poor in nutriment contain the small brown form of *Botryococcus*, whilst in waters rich in nutriment it is always represented by a red form. The latter conclusion is not supported by observations I made on Windermere during the summer of 1941, when a number of red colonies occurred. The proportion of red to green colonies increased steadily from the beginning of August, while the concentration of various nutrient salts (nitrates, phosphates, silicates, iron salts and organic matter) was falling. The concentrations of nitrate nitrogen at various parts of the lake varies from 0·43 to 0·1 p.p.m. at the beginning and from 0·19 to 0·05 p.p.m. at the end of August; the average concentrations of ammoniacal nitrogen, soluble phosphorus, iron, silica and calcium carbonate during August were 0·082–0·016, 0·007–0·0002, 0·19–0·12, 0·88–0·38 and 1·64–0·65 respectively. The water of Windermere during August 1941 was thus hardly rich in nutriment, as the concentrations of dissolved substances were mostly much below the average of natural waters as estimated by Murray (1887) and Clarke (1924; see also footnote on p. 116, and Chu, 1942, p. 304, Table 7). No red-coloured *Botryococcus* has ever appeared in the many cultures with different concentrations of inorganic salts undertaken in the course of this work. Its occurrence must, therefore, depend on other factors.

Prof. Pearsall has informed me that according to his experience *Botryococcus* in nature is at first green and later red. He is of the opinion that this is probably due to accumulation of sugars accompanied by pigment formation, and that the light intensities utilized in this research were too low to produce this result.

On the other hand, the development of *Botryococcus* in different parts of Lake Windermere was definitely related to the nitrogen concentration, though wind action tended to distribute the colonies uniformly. The amount of *Botryococcus* found in reed swamps with a higher nitrogen concentration than other parts of the lake was always noticeably greater than in other regions. A stratum of large green *Botryococcus* colonies, with large embedded cells, was observed over the bottom mud in these reed swamps in July before they occurred in noticeable quantity in the surface layer of the water. The sum of the nitrate and the ammonium nitrogen in the water just over the mud surface at that time was 0·65 p.p.m. which is well above the lower limit for an optimum growth.

In cultures 9–11 of Exp. 23 with nitrogen concentrations of 6·9 p.p.m. upwards, the colonies tended to remain at the bottom of the tube. In 11 all the colonies occupied the bottom during the first 3 months, but, as the nitrogen concentration in the solution decreased, more and more of them floated into the supernatant liquid and at the end of

6 months none remained at the bottom. All the sedimented colonies were large and provided with compactly arranged green cells possessing thick cup-shaped chromatophores, and only little space was left for the impregnating oil. Their high specific gravity is no doubt a result of the compact aggregation of the cells.

A duplicate set of similar cultures was made in medium 13, with varying amounts of $(NH_4)_2SO_4$ in place of KNO_3. They were exposed to the same conditions as the other series. The result was comparable to that obtained with the KNO_3 series, but the growth in corresponding cultures was definitely poorer and the colonies were much smaller. This confirms the conclusion drawn from Exp. 12 (Chu, 1942, p. 314) that nitrate is a better source of nitrogen than ammonium for the growth of *Botryococcus*, though the latter can utilize nitrogen directly from ammonium, as shown by a parallel series of non-phosphate cultures made at the same time and in which no noticeable nitrification took place (cf. p. 111).

(*d*) **Nitzschia palea** Kütz.

Exp. 24. Media 5 (series A) and 6 (series B), with the nitrogen-containing salts varying from 0·1 to 100 p.p.m. as in Exp. 18, in eight duplicate 10 c.c. cultures, illuminated 7 hr. daily in apparatus C at a distance of 1·5 ft. from the source of light; inoculum approximately 1000 cells. The relative density of the populations, in cultures with different nitrogen concentrations in one set of series B, is shown in Fig. 13, *N* 1, *N* 2 and *N* 3, as estimated by turbidity measurements at different periods.

The first four cultures of series A and the first three of series B showed very poor growth from the beginning, the best growth during the early period (about 3 weeks) being obtained in cultures 5 and 6 of series A and 4–6 of series B (Fig. 13, *N* 1). The range of optimum nitrogen concentration is thus narrower in series A with $(NH_4)_2SO_4$ as the source of nitrogen. The upper limit of the optimum concentration in this series is probably somewhere between that in cultures 6 and 7, the inhibiting effect in 7 being very slight. In series B the optimum range seems to be from 1·3 to 6·5 p.p.m. (Fig. 13, *N* 1); the lower limit may be a little below 1·3 p.p.m., i.e. somewhere between the concentrations of cultures 3 ($N = 0{\cdot}26$ p.p.m.) and 4 ($N = 1{\cdot}3$ p.p.m.).

There is an increasing inhibiting effect in both series in cultures with a nitrogen concentration exceeding 10·6 p.p.m., and this is very marked when the concentration reaches 26·2 p.p.m. The effect later diminishes and ultimately disappears in the usual way in cultures with 10·6 and 13·1 p.p.m. of nitrogen, and after 3 months (Fig. 13, *N* 3) these showed the best growth at a time when the inhibiting effect in higher concentrations, though markedly diminished, still persisted.

(*e*) **Fragilaria crotonensis** Kitton

Exp. 25. Media 5 (series A) and 6 (series B), with the same range of concentrations of the nitrogen-containing salts as in Exp. 18; duplicate cultures exposed to the same conditions as in Exp. 24; inoculum three drops from a culture in medium 5, one drop containing 1050 cells on the average. The growth in the different cultures of one set of series B after 24 (*F* 1) and 95 (*F* 2) days, as expressed by turbidity measurements, is shown in Fig. 13.

The duplicate cultures corresponded well. The range of nitrogen concentration for an optimum growth of *Fragilaria* seems to be wider than that for *Nitzschia*, being about

0·26–1·3 p.p.m., there being no significant inhibiting effect in the latter concentration. In concentrations from 21·2 p.p.m. upwards such an effect is very marked during the first 3 weeks, although later steadily diminishing but still noticeable at the end of the experiment (95 days). The first two cultures in both series showed very poor growth, while during the first 24 days about equally good growth was shown by cultures 3–7. After that the growth in 4–7 in the usual way exhibited a greater increase than in 3.

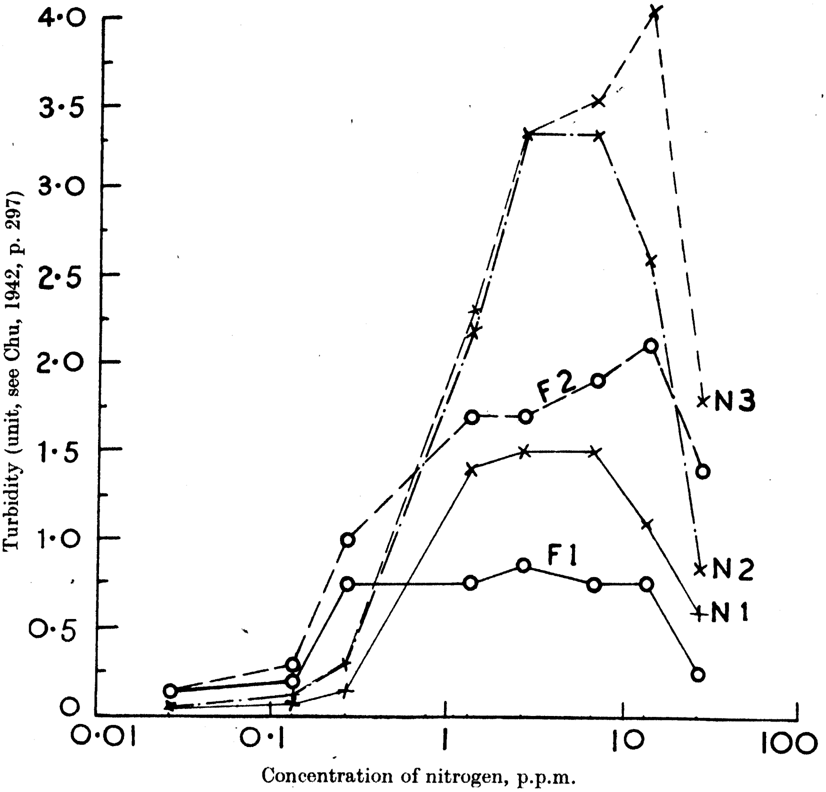


Fig. 13. Growth of *Nitzschia palea* (Exp. 24) and *Fragilaria crotonensis* (Exp. 25) in various nitrogen concentrations: *N* 1, *N* 2 and *N* 3, *Nitzschia palea*, 23, 40 and 101 days respectively, of one set of series B; *F* 1 and *F* 2, *Fragilaria crotonensis*, 24 and 95 days respectively, of one set of series B; turbidity.

(*f*) **Asterionella gracillima** (Hantzsch) Heib.

Exp. 26. Medium 9 with nine concentrations of $Ca(NO_3)_2$, viz. (1) 0·1, (2) 0·5, (3) 1·0, (4) 3·0, (5) 5.0, (6) 10, (7) 50, (8) 100 and (9) 500 p.p.m. (N = 0·017, 0·085, 0·17, 0·51, 0·85, 1·7, 8·5, 17·1 and 85·4 p.p.m.) in duplicate 10 c.c. cultures; one series (A) illuminated in apparatus C for 7 hr. daily at a temperature of 22 ± 2° C. and at a distance of 14 in. from the source of light, the other (B) illuminated 24 hr. daily at a temperature of 9 ± 1° C. for the first 26 days and then treated in the same way as A. The growth in the different cultures of series A and B (average of the two sets), as estimated by turbidity measurements, is shown in Fig. 14.

In both series there was hardly any growth in cultures 1 and 2 and very little in culture 3. During the first 2 weeks approximately equal growth took place in cultures 4–8

(Fig. 14, *A*, *B*), while later the rate of growth decreased successively in cultures from 7 to 4 as the concentration fell (Fig. 14, *C*, *D* and *E*). During the first month the growth in culture 9 was very poor, but the rate of multiplication later increased, though an inhibiting effect was still noticeable at the end of the experiment (2 months). The *Asterionella* colonies in this culture generally consisted of a large number (mostly 12) of cells which were on the average slightly broader and shorter than those in the other cultures.

The effect of illumination is conspicuous (cf. Fig. 14, *A*, *B*) and the growth in series B was much quicker during the period of continuous illumination; after removal to the same illumination as that supplied to series A, the difference between the growth of corresponding cultures soon became progressively less marked.

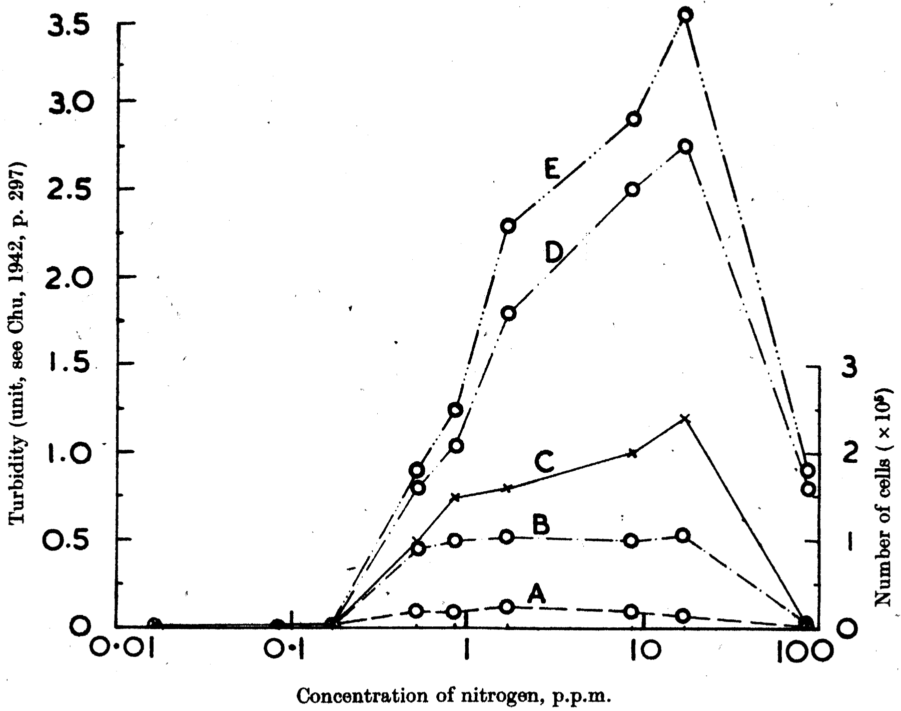
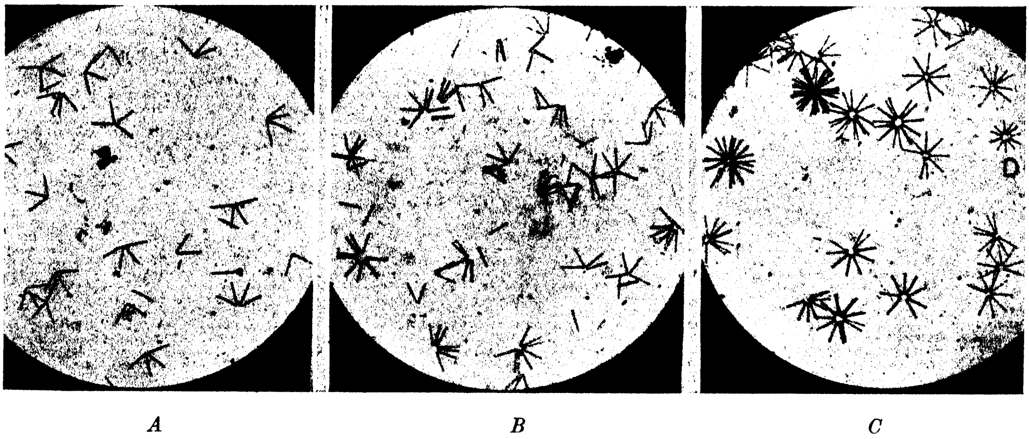


Fig. 14. Growth of *Asterionella gracillima* (Exp. 26, medium 9) in various nitrogen concentrations: *A* and *B*, 16 days of series A and B respectively, turbidity; *C*, 26 days, series B, number of cells; *D* and *E*, 55 days, series A and B respectively, turbidity.

The lower limit of nitrogen concentration for an optimum growth under the conditions of this experiment is about 0·51 p.p.m., while the upper is about 17·1 p.p.m. There is a marked inhibiting effect when the nitrogen concentration reaches 85·4 p.p.m. In different concentrations of nitrogen there are certain differences in the morphology of the *Asterionella* colonies and especially in the number of component cells. Table 25 shows the distribution of colonies with different numbers of cells in one set of cultures of series B, 25 days after inoculation. The average number of cells per colony increases with increasing nitrogen concentration, while the number of single-celled colonies decreases with increasing concentration. In cultures 4 (Fig. 15, *A*) and 5 the number of cells in the colony is mostly 2–4, in 6 (Fig. 15, *B*) mostly 4–8, in 7 mostly 8, and in 8 (Fig. 15, *C*) mostly 8–14. Some colonies in cultures 7 and 8 had no less than 22 cells, and in some of these the cells were arranged in double layers with one ring over the other (Fig. 15, *C*). Colonies with three layers of cells were also frequently observed.

Table 25. *Relation between concentration of* $Ca(NO_3)_2$ *and the number of cells in the colonies of* Asterionella (*Exp.* 26, *medium* 9)

No. of cells in colonies	Percentage of colonies with different numbers of component cells					
1	11	8	6	4	0	Colonies with 3 to 14 cells, mostly 12
2	25	26	3	2	0	
3	7	14	4	1	0	
4	50	28	14	8	2	
5	4	4	6	2	0	
6	1	8	10	2	3	
7	0	6	10	4	11	
8	2	4	16	20	13	
9	0	2	6	4	7	
10	0	0	5	6	9	
11	0	0	4	4	7	
12	0	0	3	8	11	
13	0	0	4	2	7	
14	0	0	4	10	17	
15	0	0	2	8	6	
16	0	0	1	8	1	
17	0	0	2	0	0	
18	0	0	0	1	0	
19	0	0	0	0	0	
20	0	0	0	0	2	
21	0	0	0	2	1	
22	0	0	0	4	3	
Cultures	**4**	**5**	**6**	**7**	**8**	**9**
No. of cells per c.c.	98,400	147,350	148,400	151,600	244,000	106
Conc. of $Ca(NO_3)_2$ p.p.m.	3	5	10	50	100	500
Conc. of N p.p.m.	0·51	0·85	1·7	8·5	17·1	85·4
Av. no. of cells per colony	3·2	3·7	7·4	10·5	11·2	12



A *B* *C*

Fig. 15. Variation in the number of cells of *Asterionella* colony grown in cultures with different nitrogen concentrations (Exp. 26): *A*, culture 4, N = 0·51 p.p.m.; *B*, culture 6, N = 1·7 p.p.m.; *C*, culture 8, N = 17·1 p.p.m., **D** being a dwarf colony.

There is often a marked variation in the number of constituent cells in *Asterionella* colonies in nature. In three London reservoirs Gardiner (1941*b*) found that the average number of cells per *Asterionella* colony steadily decreased from February onwards; there were 6·9 cells on 20 February, 5·7 on 5 March, 3·6 on 19 March, and 2·1 on 2 April.

Gardiner suggests that this decrease in the mean number of cells per colony is to be correlated with an increased rate of multiplication, and this is evident in the early part of the period of observation. The number of cells per c.c. of reservoir water, however, fell from 14,960 on 19 March to 690 on 2 April, while the average number of cells per colony still decreased from 3·6 to 2·1. The nitrogen concentration in these reservoirs generally decreases from spring to summer, and in the light of the results obtained in Exp. 26 it seems not improbable that a fall in nitrogen concentration may be a factor causing the decrease in number of cells per colony observed by Gardiner. The increase to an average of 6·8 cells from October until the following February may be in part determined by the high nitrogen concentration usually obtaining at this period.

The length of the *Asterionella* cells is also to some extent related to the nitrogen concentration of the solution. All the cells in cultures 4 and 5, and most of those in 6–9, are 53 μ long, though in 8 and 9 the cells of certain colonies are slightly shorter (50–52 μ). In cultures 6–9, moreover, there are colonies with dwarf cells (Fig. 15, *C*, **D**), and the percentage of such colonies increases with increasing nitrogen concentration; in culture 6 they constitute less than 1 % of the whole; in 7 and 8, 1·5 and 2·4 % respectively; and in 9 more than 3 %. These short cells vary between 29 and 35 μ in length, being mostly 32 μ long.

Exps. 24–26 show that the growth of the diatoms investigated is favoured by an increase in the amount of inorganic nitrogen up to a certain upper limit which will hardly be reached in the surface layers of natural waters. No good growth was ever obtained in solutions with nitrogen concentrations less than 0·1 p.p.m. The lower limit for an optimum growth differs slightly for different species; for *Fragilaria crotonensis* it is about 0·26 p.p.m., for *Asterionella gracillima* about 0·5 p.p.m., and for *Nitzschia palea* about or below 1·3 p.p.m. The upper limit of nitrogen concentration, beyond which there is a significant inhibiting effect, is about 6·5 p.p.m. or probably a little higher for *Nitzschia palea*, and 17 p.p.m. for the other two diatoms. Since the concentration of inorganic nitrogen in natural waters is mostly below 5 p.p.m. and rarely exceeds 13 p.p.m., an inhibiting effect of excessive nitrogen on the growth of plankton diatoms is improbable.

Generally speaking the optimum range and the range of nitrogen concentrations that can be tolerated is wider for the diatoms than for *Pediastrum* and *Staurastrum paradoxum*, especially the former. The lower limit for optimum growth for the diatoms and *Botryococcus* is lower than that for the green algae. In waters in which the nitrogen concentration frequently fluctuates between 0·26 and 1·3 p.p.m. the development of diatoms may therefore be less affected by a rise and fall of nitrogen than that of *Pediastrum* or *Staurastrum paradoxum*.

The importance for the development of diatoms of the amount of nitrogen present was noted nearly half a century ago by Whipple (1894). Kofoid (1908), however, found little correlation between the fluctuations of nitrates and the growth of diatoms and suggested that this might be due to sewage contamination resulting in an amount of nitrate far in excess of that necessary for the growth of diatoms. Such an explanation may well be justified in waters in which the inorganic nitrogen always remains above the lower limit for optimum growth. In the River Illinois, however, the nitrogen concentration varies from well above to well below the lower limit for optimum growth of *Asterionella gracillima* and *Fragilaria crotonensis*, and some effect of this fluctuation on their development is to be expected.

Fig. 16, plotted from Kofoid's data (1903, p. 603; 1908, p. 317), shows the frequency of these two diatoms in relation to the monthly average of nitrate in the Illinois during 1898; the number of cloudy days is shown by the dotted area at the top of the figure. It is evident that *Asterionella* decreases as the nitrate falls after April; the unusual drop in May must be due to other factors, possibly to the increased number of cloudy days, since Exp. 26 shows that the development of *Asterionella* is favoured by increased light. In July and August, when the nitrate falls to as low as 0·2 and 0·05 p.p.m., *Asterionella* is very poorly represented, but slight growth recommences at the end of November when the nitrate increases to 1·25 p.p.m. (N = 0·28 p.p.m.). *Fragilaria crotonensis* increased in April up to early May, but disappeared in June following the fall of nitrate to 0·75 p.p.m. (N = 0·17 p.p.m.). Judging by these data the lower limit of nitrogen concentration for optimum growth in the Illinois seems to come very near to that determined in my experiments. The very poor growth in February, when the nitrate content is highest, must be due to the low light intensity at that time of the year, an effect accentuated by the considerable number of cloudy days. The increase of *Asterionella* from March to April

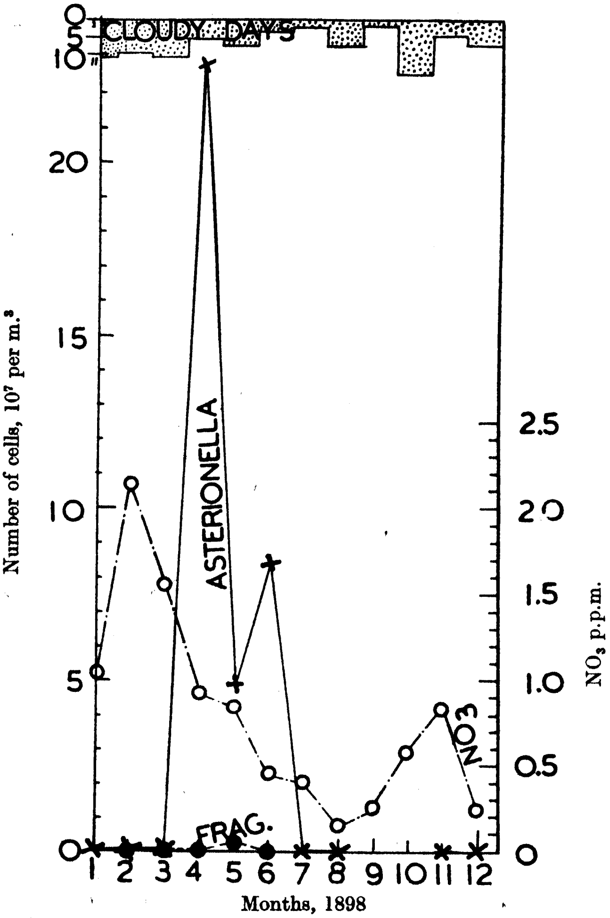


Fig. 16. Correlation of the growth of *Asterionella gracillima* and *Fragilaria crotonensis* with the concentration of nitrate in the River Illinois, 1898, based on Kofoid's data.

was not due to the fall of nitrogen concentration but to the better illumination. In the same way the poor growth in the London reservoirs (Gardiner, 1941*b*) during winter (*ca.* 87 cells per c.c.), when the nitrogen concentration is usually high, must be due to light deficiency, and the increase from February to March (from 523 to 14,960 cells per c.c.) to the increasing illumination.

In the English lakes *Asterionella* shows an appreciable development only in those with a higher nitrate content, and Pearsall's data (1930, 1932) indicate that the increase and decrease of *Asterionella* is often to some extent correlated with the rise and fall in nitrates. In Derwentwater (see Fig. 22, *A*) *Asterionella* disappears after the nitrate nitrogen falls to 0·005 p.p.m. in July, and begins to increase from September following a rise in the nitrate nitrogen. In Bassenthwaite and Ullswater (Fig. 22, *B*, *C*) increase of nitrate from August onwards is accompanied by increase of *Asterionella*; the fall of nitrate after June in Ullswater is followed by a decrease of *Asterionella*. Hence a fluctuation in the development of diatoms according to the pulse of the nitrate content of the water is to be expected, unless other factors come into play.

In the Barn Elms Reservoir, with soluble phosphorus above the lower limit for optimum growth for most of the year, the effect of nitrogen concentration on the growth of diatoms is more evident. In 1938, when the nitrate nitrogen fell from 0·4 to 0·1 during the period from March to June (Metropolitan Water Board, 33*rd Ann. Rep.* pp. 30 and 108; Fig. 23, p. 189), there was a rapid fall of the diatom plankton (Gardiner, 1941*a*, Table 1). The effect may be accentuated by phosphorus deficiency during April and May. Though there was a considerable increase of phosphorus from June onwards, the diatom population remained low owing to the limiting influence of nitrogen deficiency. A slight increase took place during September and October when the nitrate nitrogen increased from an undetectable quantity in August to 0·2 p.p.m. in September; after this the growth was again checked because of the fall of nitrate nitrogen to 0·1 p.p.m. during October and November. The increase of nitrogen in December was immediately followed by an increase of diatom plankton in January.

(*g*) *General consideration of the influence of nitrogen concentrations on the growth of the organisms studied*

Exps. 18–26 show that there is an optimum range of nitrogen concentrations most suitable for the growth of each plankton. The development of all the planktons studied can be limited by a nitrogen deficiency when the nitrogen concentration of the medium is below the lower limit of this optimum range, and below this limit their development is beneficially affected, as in higher plants, by an increase of nitrogen. On the other hand, there is a definite inhibiting effect when the nitrogen concentration exceeds an upper optimum limit, and above this limit the development is unfavourably affected by an increase, but favourably affected by a decrease of the nitrogen concentration. The inhibiting effect becomes more and more marked, the more the nitrogen concentration exceeds the optimum range. There is some slight difference in the optimum range for the different forms, the lower limit varying from about 0·26 to about 1·3 p.p.m. or, in the case of *Staurastrum paradoxum*, possibly to 2·6 or 5·3 (when ammonium is the source of nitrogen) p.p.m., and the upper from about 6·5 to about 17 p.p.m. Optimum growth is shown by all the organisms studied with the only possible exception of *Staurastrum paradoxum*, for which the optimum range of concentrations of ammoniacal nitrogen may be narrower than the range 1·3–6·5 p.p.m., if other conditions are suitable, when the nitrogen concentration (as ammoniacal or nitrate nitrogen) is between 1·3 and 6·5 p.p.m. Generally speaking the lower limit for optimum growth for green algae (0·69–1·3, or more, p.p.m.) seems to be a little higher than that for *Botryococcus* and for the diatoms (0·26–0·51 p.p.m.), with the probable exception of *Nitzschia palea*, the lower limit for which seems to be about 1·3 p.p.m. or probably somewhere between 1·3 and 0·26 p.p.m. *Pediastrum boryanum* is less tolerant than others of higher nitrogen concentrations from 69 p.p.m. upwards.

All the organisms studied can utilize both ammoniacal and nitrate nitrogen, although the relative nutritive value of the two types differs to some extent. Thus, the growth of *Botryococcus* in solutions with ammonium salts as the only source of nitrogen is always inferior to that in solutions with nitrates, while the other organisms show equally good growth within the optimum range of nitrogen concentrations whether supplied with ammonium salts or nitrates. The optimum range is generally narrower for ammoniacal than for nitrate nitrogen. The lower limit of optimum range is always higher when ammonium salts are used.

The development of the forms studied is not noticeably affected by increasing or decreasing the nitrogen concentration, as long as it remains within the optimum range. In cultures that are not continuously replenished, however, the nitrogen concentration of course gradually falls and ultimately comes to be below the lower limit of the optimum range, and as soon as this happens the rate of multiplication decreases. A similar change occurs in cultures which are not far above the optimum range and in which, although growth is retarded, but not entirely inhibited, at first, a concentration is sooner or later reached which is nearer to and ultimately within the optimum range (Figs. 10–14). But, if the concentration is so high that a particular organism undergoes practically no growth (as in the last culture of Exp. 20), the initial inhibiting effect persists. The ultimate development in a series of cultures is therefore proportional to the initial nitrogen concentrations in the respective cultures, and the final growth, if other factors are suitable, is most considerable in the culture with the highest initial nitrogen concentration unless the inhibiting effect in this culture persists throughout the whole period of the experiment, as in culture 10 of Exp. 20 (Fig. 10, p. 114).

Since the concentration of inorganic nitrogen in ordinary waters is usually below 5 and rarely exceeds 13 p.p.m., a marked inhibiting effect in nature is improbable. Since, however, the concentration frequently falls below the lower limit of the optimum range, nitrogen deficiency must frequently operate as a limiting factor. In the English lakes the nitrogen concentration is always below the lower limit for optimum growth of all the planktons here studied. It is very likely therefore that nitrogen deficiency is a limiting factor for the phytoplankton as a whole, although this may be further limited by other factors such as phosphate and light deficiencies. Thus, during winter the limiting effect of light intensity will not allow of the development of phytoplankton to the extent that the comparatively higher nitrogen concentration might permit.

Green forms often follow diatoms in summer in the English lakes when the nitrogen concentration is specially low (Pearsall, 1932), but in the light of these experiments it seems improbable that the former have a preference for the lower nitrogen concentrations than those supporting a good growth of diatoms. There is no indication whatsoever that the green forms studied are more capable than diatoms of utilizing nitrogen from low concentrations. It may be that the greater light intensity in summer is more favourable for the development of green forms than for that of diatoms.

Wiebe's (1930, 1931) conclusion that, in certain fish ponds and in the Mississippi, inorganic nitrogen is not a limiting factor is not in agreement with the results of my experiments. The sum of the ammoniacal and the nitrate nitrogen in the fish ponds he studied at various periods varies from 0·02 (pond C1, 27 July) to 0·632 (pond C2, 9 Aug.; decreased to 0·156 p.p.m. in the next analysis on 20 Aug.) p.p.m. and generally fluctuated much below, though in some fertilized ponds occasionally reaching the lower limit of the range for optimum growth of the planktonts as established by the experiments detailed above. The plankton growth could thus be limited by nitrogen deficiency and markedly affected by the rise or fall of the nitrogen concentration in those ponds during most of the time, unless it is further limited by other factors. The invariable presence of inorganic nitrogen in occasional samples, taken during two years from certain parts of a large river such as the Mississippi, is likewise scarcely sufficient to prove that it has no limiting effect on plankton growth. The lowest concentration of nitrate nitrogen in Wiebe's analyses is 0·051 p.p.m., which is approximately that in Windermere at the time of summer depletion (0·048 p.p.m., Pearsall, 1930), while the highest is 0·914 p.p.m. together with 0·224 p.p.m. ammoniacal nitrogen, the sum being just above or about the lower limit for an optimum growth of the planktonts. The growth of plankton algae in the Mississippi may therefore be expected to be affected to a marked extent by the variation in nitrogen concentration which exhibits a range larger even than that in cultures 2–5 of Exps. 22, 23 and 26 in which the growth varied from nothing to an optimum. The nitrogen concentration of the Mississippi is from 0·033 to 0·064 p.p.m. as calculated from Clarke's data (1924) while McHarque & Peter's (1921) data show that nitrate may be completely absent (Minneapolis sample); the limiting effect of nitrogen concentration must therefore be even more than is to be expected from Wiebe's data.

Wiebe's data, however, suggest that at certain times (e.g. April 1930) it was not the nitrogen concentration that was limiting plankton growth, but the depletion of phosphate which would considerably diminish the growth, even if the supply of nitrogen were adequate. It is under such conditions, when one or more other factors are restricting the growth of plankton organisms, that the limiting effect of nitrogen concentration in natural waters may be obscured.

Greater growth is, however, to be expected in natural waters, when the nitrogen concentration is below the lower limit, than in cultures with a similar nitrogen concentration, since in the former there is a much larger body of medium available and the supply of nitrogen is made good by diffusion from the deeper layers which may have a higher nitrogen concentration. There may also be replenishment from the mud. As compared with the condition in a small culture vessel the much larger volume of water to be drawn upon will probably cause the effects of nitrogen consumption to be felt more slowly.

Certain phenomena observed in these experiments are comparable to those recorded for higher plants. Thus Russell & Watson (1940; also Preston, 1941, p. 583) showed that beyond a certain range increase of nitrogen had no effect on the growth of the wheat plant; and above this range, increased nitrogen exerted an unfavourable effect. This recalls the results obtained with the planktonts here studied. Another resemblance is seen in the yellowing and discolouring effect resulting from nitrogen deficiency (Miller, 1938, p. 643). Green algae and *Botryococcus* change their colour to yellow and then to white, while diatoms show a gradual decrease in the intensity of the yellow coloration, as nitrogen becomes more and more deficient. This phenomenon is also well shown by blue-green algae (Geitler, 1936, p. 8).

II. THE INFLUENCE OF PHOSPHORUS CONCENTRATION

Atkins (1923) and Atkins & Harris (1924) found a direct correlation between the amount of phosphate and the growth of fresh-water plankton, and suggested that 'lack of phosphate rather than lack of nitrate or ammonium salts limits the plankton as a general rule in fresh water' (Atkins & Harris, 1924, p. 19). Fischer (1924) and Wiebe (1930) both concluded that soluble phosphorus may at times become a limiting factor for plankton growth in fish ponds; and Wiebe (1931) arrived at the same conclusion in his investigation of the Mississippi. The quantitative studies, made in a large number of Wisconsin lakes by Juday, Birge, Kemmerer & Robinson (1927), and Juday & Birge (1931), did not, however, produce any positive evidence of correlation between phosphate phosphorus and the production of plankton, nor indicate that the former is a limiting factor in the development of the latter. Wimmer (1929) and Tressler & Domogalla (1931) also failed to find a definite correlation between phosphorus and the amount of plankton growth.

Recently, Mortimer (1939), studying plankton production in Windermere, finds that 'phosphate is more often a limiting substance than nitrate'. Riley (1940, p. 295), in Linsley Pond, concluded that 'phosphate, having a correlation with chlorophyll that is significant to 1 per cent level of probability, is the more important limiting factor', while 'the immediate effect of nitrate is negligible'. On the other hand, Harris & Silvey (1940, pp. 123, 124) do not recognize any correlations between plankton growth and concentrations of phosphate and nitrate. Gardiner (1941 *a*), in correlating the occurrence of diatoms with the chemical composition of the water, concludes that 'some factor other than the concentration of phosphorus and silica, must be decisive'.

These conflicting results render a definite conclusion impossible. In the waters studied other chemical, environmental and meteorological factors are operative. The effects of changing concentrations of phosphate phosphorus on the development of plankton algae, like that of nitrogen, can only be solved experimentally with unialgal cultures in which all the other factors are controlled. The experiments described below were carried out with this object in view.

(*a*) **Pediastrum boryanum** (Turp.) Menegh.

Exp. 27. Medium 6, with K_2HPO_4 (1) 0·1, (2) 0·5, (3) 0·75, (4) 1·0, (5) 2·5, (6) 5·0, (7) 7·5. (8) 10, (9) 50 and (10) 100 p.p.m. ($P=0{\cdot}018$, 0·089, 0·13, 0·18, 0·45, 0·89, 1·34, 1·78, 8·9 and 17·8 p.p.m. respectively) in ten duplicate 50 c.c. cultures; one series (A) illuminated 7 hr. (23 ± 1° C.) and another (B) 24 hr. daily in illuminating apparatus C. Inoculum 5 drops from a 13 days' old culture of series B (6), Exp. 19, just reaching maximum growth, one drop containing on the average 550 colonies, mostly 26–32μ in diameter. The results of one set of series A (Fig. 17, 1, 3 and 5) and series B (Fig. 17, 2, 4 and 6) as determined by turbidity measurements at different periods are shown in Fig. 17.

The relative growth in the different concentrations of phosphorus shows considerable similarity in both series, though that in series B was in general greater, especially during the first weeks (cf. Fig. 17, 1 with 2, and 3 with 4). This difference in the amount of growth between corresponding cultures of the two series is no doubt due to the different periods of illumination. After 8 weeks there was not much difference between the two series in cultures 2–7, although in 8–10 it was more pronounced. At that time the inhibiting effect in cultures 8–10 of series A was still marked, while in B it had completely disappeared in culture 8 and was only very slight in 9 and 10. After 10 weeks and up to the end of the experiment (288 days) there was a slight but distinct difference between the growths of the two series only in the last two cultures (Fig. 17, 5 and 6); in the other corresponding cultures the growth was identical.

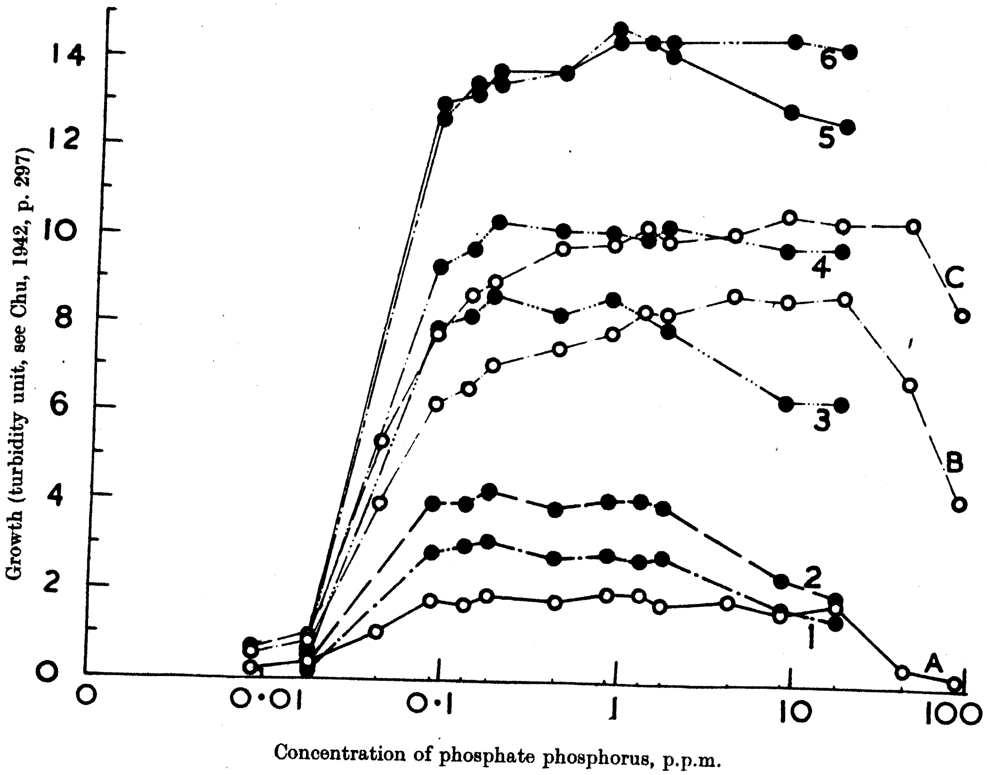


Fig. 17. Growth of *Pediastrum Boryanum* in different concentrations of phosphate phosphorus in Exps. 27 (curves 1–6) and 28 (curves *A*, *B* and *C*), expressed as turbidity: curves 1 (13 days), 3 (28 days), and 5 (288 days), series A; curves 2 (13 days), 4 (27 days) and 6 (288 days), series B; curves *A*, *B* and *C*, growth in 8, 23 and 157 days respectively.

Within either series there was no noteworthy difference in the amount of growth during the first 2 weeks in cultures 2–8, in all of which the concentrations of phosphorus seemed adequate for an optimum growth. In culture 1 the growth was exceedingly poor from the very beginning, evidently as a result of phosphorus deficiency. In the last two cultures there was at first a distinct inhibiting effect, the growth being much inferior to that in cultures 2–8, but this effect gradually decreased in the usual way. The range of phosphorus concentration for an optimum growth of *Pediastrum boryanum* in this experiment seems, therefore, to be from 0·089 to 1·78 p.p.m. Phosphorus deficiency will show itself below this range, and an inhibiting effect above it.

The shift of optimum growth to cultures with higher initial phosphorus concentrations took place more slowly and on a smaller scale than in Exps. 18–26 with different nitrogen concentrations. At the end of the experiment, cultures 6–8 of series A and 6–10 of series B were the best, while cultures with lower initial phosphorus concentrations were inferior, though the differences between successive cultures was slight as compared with that in Exps. 18–26. In all the cultures, including those with high phosphorus concentrations and evidently not suffering from any phosphorus deficiency, the growth rate decreased rapidly after 4 weeks, which must be due to the limiting effect of one or more other factors, the most important of which is probably depletion of nitrogen; the only exception was constituted by the first culture where the growth was seriously limited from the beginning by phosphorus deficiency.

The influence of length of illumination was particularly noteworthy during the first 2 weeks in cultures (e.g. 2–8) containing optimum concentrations of both phosphorus and nitrogen, but this influence decreased as deficiency in nitrogen or phosphorus or in both came into play. No effect of the length of illumination was recognizable during the final periods of this experiment, the growth in corresponding cultures 2–8 of the two series being about the same (cf. Fig. 17, 5 and 6). At this stage the nitrogen in these cultures must have been nearly exhausted, and the growth rate possible with such a low nitrogen concentration would be much less than that possible owing to the shorter length of illumination of the cultures in series A; it is therefore comprehensible that the longer period of illumination in series B did not result in any difference in the growth. There was, however, an evident difference in the total amount of growth between the two series in the last two cultures, but here the more abundant growth in cultures 9 and 10 of series B seems to be due to the earlier cessation of the inhibiting effect of the high initial phosphorus concentrations as a result of the longer illumination in earlier periods. As a matter of fact, the growth rate in cultures 9 and 10 of series A was greater during the final periods, as can be seen from the fact that the difference in the amount of growth between the two series in these two cultures was much smaller at the end of the experiment than when the cultures were only 4 weeks old and presumably not suffering from any marked nitrogen deficiency. The growth rate of the last two cultures showed an earlier and more rapid decrease in series B than in series A, because nitrogen deficiency arose earlier in B owing to the better growth and more rapid consumption.

Exp. 28. Medium 10 with K_2HPO_4 (1) 0·05, (2) 0·1, (3) 0·25, (4) 0·5, (5) 0·75, (6) 1·0, (7) 2·5, (8) 5·0, (9) 7·5, (10) 10, (11) 25, (12) 50, (13) 100, (14) 250 and (15) 500 p.p.m. ($P = 0·0089$, 0·018, 0·045, 0·089, 0·13, 0·18, 0·45, 0·89, 1·34, 1·78, 4·45, 8·9, 17·8, 44·5 and 89 p.p.m. respectively) in fifteen duplicate 50 c.c. cultures, illuminated 7 hr. daily in apparatus C; inoculum approximately 100 colonies per c.c. The growth of one set of cultures, as estimated by turbidity measurements at three stages, is shown in Fig. 17, *A*, *B* and *C*.

During the first 10 days the best growth occurred in cultures 4–13 with 0·089 to 17·8 p.p.m. of phosphorus, while in lower concentrations the growth decreased and in higher ones an inhibiting effect (Fig. 17, *A*) was recognizable. The lower limit of phosphorus concentration for an optimum growth therefore seems, as in Exp. 27, to be approximately 0·089 p.p.m., while the upper limit is about 17·8 p.p.m. which is much higher than in Exp. 27. The subsequent changes in the cultures followed the same course as in Exp. 27, though taking place more rapidly, probably because of the larger inoculum. The best growth at the end of the experiment (157 days) was in cultures 12–14. There was a serious inhibiting effect in the last two cultures in the early part of the experiment (Fig. 17, *A*), but this gradually decreased, though it remained noticeable in the last culture even at the end of the experiment.

A decrease in the rate of growth was again noticeable after 12 days in all but the last two cultures, and after 23 days growth in most of them had nearly ceased. This is probably due to nitrogen deficiency in cultures 6–13 with a high initial phosphorus concentration, but no doubt mainly due to phosphorus deficiency in cultures 1–5. Both factors may have operated in some cultures (probably in 6–11). In culture 14 the rate of growth steadily increased during the first 3 weeks, no doubt as a result of the decreasing inhibiting effect of the high initial concentration; subsequently it gradually decreased. In culture 15 the growth rate began to decrease after 4 weeks.

The most striking contrast between the results of Exps. 27 and 28 is that the upper limit of suitable phosphorus concentration in medium 10 is much higher than in medium 6 (17·8 p.p.m. in the former and 1·78 p.p.m. in the latter). The main difference between the two media lies in the nitrogenous salts present, and this may be the factor responsible for the difference in suitability of higher phosphorus concentrations.

Both experiments show that phosphorus deficiency limits the growth of *Pediastrum boryanum* when the concentration is as low as 0·018 p.p.m. or less, and that this effect is independent of the fact that nitrogen is available in an optimum concentration. A phosphorus concentration of 0·045 is still a little below the lower limit for optimum growth and therefore, if other conditions are suitable, the growth is liable to be affected. In higher concentrations, up to 1·78 p.p.m. in medium 6 and 17·8 p.p.m. in medium 10, phosphorus has no limiting effect on the growth of this alga, and increase or decrease of phosphorus does not affect the growth as long as the concentration remains within the optimum range.

The soluble phosphorus in natural waters is nearly always below 1·78 p.p.m., so that an inhibiting effect is unlikely to occur in nature. Since, however, the concentration is often below the lower limit for optimum growth during the period from late spring to autumn when conditions of illumination are favourable, phosphorus deficiency must frequently limit the growth of *Pediastrum*. Even in waters with a high phosphorus content, such as Lake Wingra (Tressler & Domogalla, 1931), the concentration is frequently below 0·05 p.p.m. and for most of the year below 0·1 p.p.m. If the frequency of *Pediastrum* in this lake is compared with the graph for soluble phosphorus, the correlation is remarkable (Tressler & Domogalla, 1931, Figs. 6, 11). The increased development in early April follows immediately on the rise in phosphorus concentration, while the gradual decrease from May onwards corresponds to the fall of phosphorus; the rise of the latter in August is immediately followed by an increase of *Pediastrum*.

(*b*) **Staurastrum paradoxum** Meyen

Exp. 29. Two series (A and B) of ten duplicate 10 c.c. cultures in medium 6 with K_2HPO_4 varying from 0·1 to 100 p.p.m. as in Exp. 27, the phosphorus concentration being (1) 0·018, (2) 0·089, (3) 0·13, (4) 0·18, (5) 0·45, (6) 0·89, (7) 1·34, (8) 1·78, (9) 8·9 and (10) 17·8 p.p.m.; A with 7 and B with 24 hr. illumination daily in apparatus C; inoculum, three drops from a culture in medium 6, one drop containing an average of

140 individuals. The growth, as expressed by turbidity measurements (average of two sets), is shown in Fig. 18.

Both series agreed in the relative growth in different phosphorus concentrations, but B developed more quickly than A in the first 7 weeks (Fig. 18, 2 and 3) after which the difference between the two series decreased. On the whole the effect of difference in length of illumination on the growth of *Staurastrum paradoxum* is comparable to that on the growth of *Pediastrum* (Exp. 27); the effect disappears as the limiting influence of nitrogen or phosphorus deficiency comes into play.

During the first 2 weeks in series B (Fig. 18, 1) and the first 4 weeks in series A the growth in cultures 2–8 was in general equally good, though in one set of series B culture 8 was slightly inferior. The strong inhibiting effect in the last two cultures was noteworthy up to the end of the experiment (216 days), though it was slightly less marked in later periods in culture 9. In cultures 1 and 10 the growth was exceedingly poor during the whole period of the experiment. Cultures 2–4 successively showed a diminution in growth in later periods as the phosphorus content decreased, but the amount of growth in cultures 5–8 remained large.

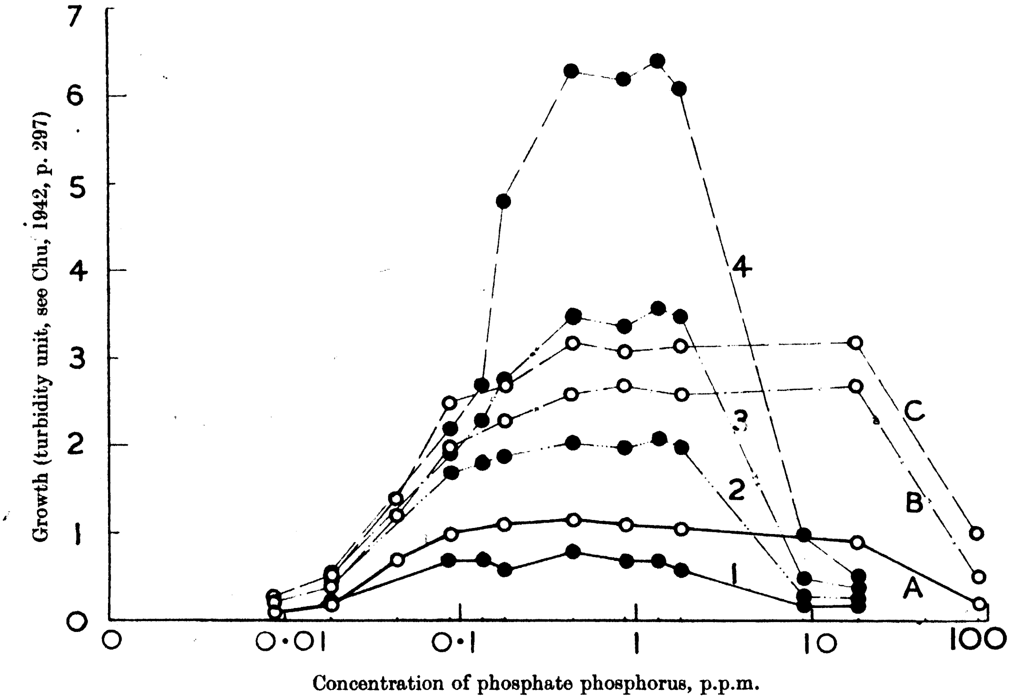


Fig. 18. Growth of *Staurastrum paradoxum* in different concentrations of phosphate phosphorus in Exps. 29 (curves 1–4) and 30 (curves *A*, *B* and *C*), expressed as turbidity: curves 1, 3 and 4, showing growth of 14, 49 and 216 days respectively in series B; curves 2, growth of 49 days in series A; curves *A*, *B* and *C*, growth of 18, 58 and 89 days respectively.

The range of phosphorus concentration for optimum growth of *Staurastrum paradoxum* in medium 6 is therefore similar to that for *Pediastrum* (Exp. 27), viz. from 0·089 to about 1·78 p.p.m., but the latter seems to tolerate high phosphorus concentrations (8·9–17·8 p.p.m.) much better than *Staurastrum paradoxum*. The inhibiting effect of such concentrations soon diminished and ultimately disappeared in the *Pediastrum* cultures, but not in those of *Staurastrum paradoxum* (cf. Fig. 17, 1–6 with Fig. 18, 1–4).

Exp. 30. Ten duplicate 10 c.c. cultures in medium 9 with $Ca(NO_3)_2$, 6 p.p.m. and K_2HPO_4 (1) 0·05, (2) 0·1, (3) 0·25, (4) 0·5, (5) 1·0, (6) 2·5, (7) 5·0, (8) 10, (9) 100 and (10) 500 p.p.m. (P = 0·0089, 0·018, 0·045, 0·089, 0·18, 0·45, 0·89, 1·78, 17·8 and 89 p.p.m.); continuous illumination in apparatus C; inoculum, three drops from a culture in medium 9, one drop with an average of 140 individuals. The average growth of the two sets of cultures, as estimated by turbidity measurements, after 18, 58 and 89 days, is shown in Fig. 18, *A*, *B* and *C*.

During the first 18 days the best growth occurred in cultures 4–9 and there was not much difference between them, though the growth in culture 9 of one set was slightly inferior. After 8 weeks cultures 6–9 showed the best growth while that in cultures 4 and 5 became successively inferior. After 53 days the growth rate dropped rapidly in all cultures except the last where it continued to increase, though very slowly, up to the 89th day; after that there was hardly any additional growth in any of the cultures up to the end of the experiment (190 days). The ultimate growth in cultures 7–9 was not larger than that in culture 6, which is probably due to the fact that cultures 7–9 suffered from nitrogen deficiency during this later period so that, despite the higher phosphorus concentrations, there was no better growth.

The definite inhibiting effect in the last culture (P = 89 p.p.m.) persisted during the whole period of the experiment, but it was not as marked as in the last culture of Exp. 29, with a phosphorus concentration of 17·8 p.p.m., as the effect diminished more markedly than in the latter culture (cf. Fig. 18, 1–4 with *A*–*C*). The growth in the first two cultures was exceedingly poor, and there was evident phosphorus deficiency in the third culture (P = 0·045 p.p.m.), though the limiting effect was less marked than in the first two.

The lower limit of phosphorus concentration for an optimum growth of *Staurastrum paradoxum* in this experiment is therefore about 0·089 p.p.m., while the upper seems to be 17·8 p.p.m. As compared with Exp. 29 the range of phosphorus concentrations supporting optimum growth is therefore extended to a higher limit. There is also a diminution of the inhibiting effect in high concentrations, since 17·8 p.p.m. exerts no marked inhibiting effect in Exp. 30, although it is detrimental to the growth of *S. paradoxum* in Exp. 29 where even a concentration of 8·9 p.p.m. causes a serious inhibiting effect. Moreover, as mentioned above, the inhibiting effect in 89 p.p.m. of phosphorus in Exp. 30 in much less marked than in 17·8 p.p.m. in Exp. 29.

There was a definite limiting effect in cultures with phosphorus concentrations below 0·089 p.p.m. in both experiments. The development of *S. paradoxum* must therefore, like that of *Pediastrum*, be frequently limited in nature by phosphorus deficiency. In the English lakes the concentration of soluble phosphorus is usually below 0·018 p.p.m., a concentration equivalent to that in culture 1 of Exp. 29 and culture 2 of Exp. 30, where the growth was very poor. In Lake Windermere the highest record is 0·04 p.p.m. (Pearsall, 1930), which is slightly lower than in culture 3 of Exp. 30. The growth of *Staurastrum paradoxum* is very poor except in Windermere (Pearsall, 1932).

(*c*) **Botryococcus Braunii** Kütz.

Exp. 31. Two duplicate series (A and B) of eight 50 c.c. cultures in medium 13 with K_2HPO_4 (1) 0·89, (2) 0·5, (3) 1·0, (4) 5·0, (5) 10, (6) 50, (7) 100, and (8) 500 p.p.m. (P = 0·018, 0·089, 0·18, 0·89, 1·78, 8·9, 17·8 and 89 p.p.m.); A with 7, B with 24 hr. daily illumination in apparatus C; inoculum, four drops from a culture in medium 13, one drop containing on the average 680 colonies (dia. 21–60 μ). The growth, as estimated by turbidity measurements after 34, 74 and 187 days of each series, is shown in Fig. 19.

The relative growths in the different cultures in the two series agree well, although the development of B was always in advance of A. This was particularly striking during the first half of the third month when the cultures were flourishing (cf. Fig. 19, *C*, *D*), and the difference between the growth of the two series was largest. The effect of the longer period of illumination was less noticeable in the earlier stages, a result quite different from that obtained with the cultures of *Pediastrum* (Exp. 27) and *Staurastrum paradoxum* (Exp. 29), where it was most obvious during the first weeks. This is probably due to the fact that the growth of *Botryococcus* is so slow that the difference resulting from the different length of illumination is not at first very obvious, although later it becomes more distinct as the amount of growth increases. The total growth in cultures 2–7 of series A after 187 days was distinctly less than that in the corresponding cultures of series B after 74 days (cf. Fig. 19, *D*, *E*). After about 11 weeks the growth rate in cultures 3–7 of series B rapidly decreased and a similar decrease was noted earlier in culture 2; at this time the growth in the last culture was still increasing, although a drop occurred at a much later stage. Corresponding cultures of series A showed a similar decrease, but it occurred about

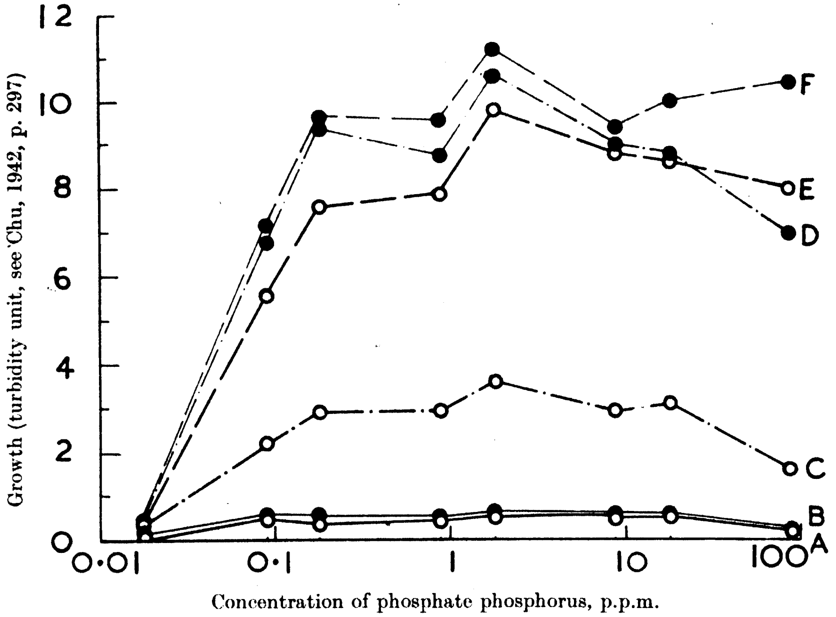


Fig. 19. Growth of *Botryococcus Braunii* Kütz. in different concentrations of phosphate phosphorus in medium 13, Exp. 31, expressed as turbidity: curves *A*, *C* and *E*, growth of 34, 74 and 187 days respectively in series A; curves *B*, *D* and *F*, growth of 34, 74 and 187 days respectively in series B.

4 months later. The decrease in the growth rate in cultures 3–9 must be largely due, as in Exps. 27–30, to nitrogen deficiency, while the earlier drop in culture 2 will have been due to phosphorus deficiency.

The growth in the first culture was very poor from the beginning. Cultures 2–7 afforded about equally good growth during the first 5 weeks in series B and about the first 7 weeks in series A, while in the last culture there was an inhibiting effect (Fig. 19, *A–D*) which diminished later in the usual way and ultimately disappeared. The lower limit of optimum phosphorus concentration for *Botryococcus*, under the conditions of the experiment, is therefore about 0·089 p.p.m., while the upper limit is about 17·8 p.p.m.

Phosphorus deficiency must often exert a limiting influence on the growth of *Botryococcus* in natural waters. In the English Lake District a noteworthy growth has been recorded only in Crummock Water during August, when the phosphorus concentration (0·003 p.p.m.) is the highest found in the English lakes. The scarcity of *Botryococcus* in Ennerdale, where there is also a high summer phosphorus concentration, is probably due to the low nitrogen content (not exceeding 0·06 p.p.m. except in December). In the late summer of 1941 an appreciable growth of *Botryococcus* occurred in Lake Windermere. The alga was first found in July near the mud surface of the reed swamps; subsequently it spread over the lake. The phosphorus concentration in the water just above the mud surface of reed swamps in Pullwyke Bay (P.W. 1*) and Sandywyke Bay (S.W. 3*) at the end of July 1941, was 0·07–0·098 p.p.m., and approximately corresponds to the lower limit of the range of phosphorus concentrations for optimum growth, established in the above experiment. The high nitrogen concentration, as mentioned above (p. 121), also encouraged the development of *Botryococcus*.

In Lake Sarah, New Zealand, *Botryococcus* is dominant in the plankton during the summer and autumn and present in all the collections (Flint, 1938). The phosphorus concentration (0·087–0·48 p.p.m.) varies from about the lower limit for optimum growth of *Botryococcus* to well within the optimum range, and this must be a factor causing its abundant growth.

The colour of the *Botryococcus* colonies is deeper in lower phosphorus concentrations within the optimum range, when the nitrogen concentration is suitable. The green colour was most intense in culture 2 and diminished in intensity in cultures with higher phosphorus concentrations, although there was not much difference between cultures 5–8 of series A during the first 15 weeks. This may be due to absorption of more phosphorus and hence of proportionally less nitrogen in the higher P-concentrations. Ketchum (1939) found that the ratio of absorption $\Delta P : \Delta N$ by the marine diatom, *Nitzschia closterium*, increased as the concentration of phosphate in the medium increased. Exp. 23 indicated that the green colour of *Botryococcus* became more intense with an increase in the available nitrogen in the medium (p. 120), and it was suggested that the increasing quantity of nitrogen absorbed affected the formation of chlorophyll. At the end of 27 weeks culture 2 remained a deep grass green, cultures 3 and 4 were slightly less deeply coloured, while 5–8 had become yellowish green. Eleven months after inoculation the colour of the cultures varied from grass green in 2 to yellowish brown in 8. The increased yellowing, which was observed in later stages in the higher phosphorus concentrations, was no doubt intensified by the decrease of nitrogen as a result of its consumption during the preceding rapid growth.

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* The places designated by P.W. 1 and S.W. 3 are shown in a map by Godward (1937, p. 498, Fig. 1*a*).

There were also morphological differences in cultures with different phosphorus concentrations. In culture 1 the colonies were small and consisted of a few cells scattered in the mucilaginous matrix which was less viscous than in the other cultures; the small thin chromatophore in the cell was very faintly coloured. *Botryococcus* colonies growing in a phosphorus-deficient medium are thus morphologically not unlike those growing in a nitrogen-deficient medium (Exp. 23). The colonies in cultures 2 and 3 resembled those in the original inoculum. In the higher concentrations there was a gradual decrease in the size of the colonies and an increase in the length of the connecting mucilage-strands, while the mucilage itself became firmer and tended to form a definite cup-shaped envelope around each cell. The size of the cell, as well as the thickness of the chromatophore, decreased slightly as the concentration became higher.

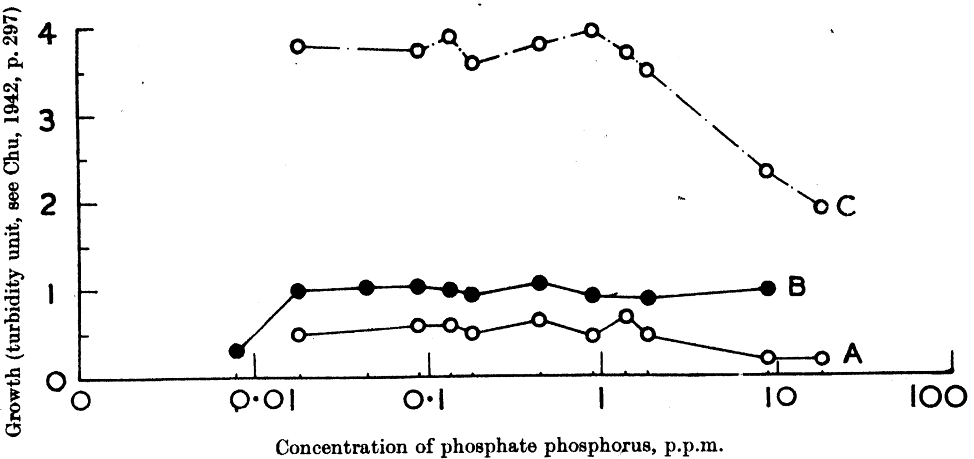

Fig. 20. Growth of *Nitzschia palea* Kütz. in different concentrations of phosphate phosphorus in medium 6 (curves *A* and *C*) and medium 9 (curve *B*), Exp. 32, expressed as turbidity: Curves *A*, *B* and *C*, growth in one set of cultures in 10, 12 and 19 days respectively.

(*d*) **Nitzschia palea** Kütz.

Exp. 32. Series 1 with duplicate sets of ten cultures (10 c.c.) in medium 6 with K_2HPO_4 varying from 0·1 to 100 p.p.m., the phosphorus concentrations being (1) 0·018, (2) 0·089, (3) 0·13, (4) 0·18, (5) 0·45, (6) 0·89, (7) 1·34, (8) 1·78, (9) 8·9 and (10) 17·8 p.p.m.; series 2 with duplicate sets of ten cultures (10 c.c.) in medium 9 with $Ca(NO_3)_2$ 20 p.p.m. and K_2HPO_4 varying from 0·05 to 50 p.p.m., the phosphorus concentrations being (1) 0·0089, (2) 0·018, (3) 0·045, (4) 0·089, (5) 0·13, (6) 0·18, (7) 0·45, (8) 0·89, (9) 1·78 and (10) 8·9 p.p.m.; illuminated 7 hr. daily in apparatus C; inoculum, three drops from a culture in medium 6, one drop containing an average of 450 cells. The growth of one set of each series, as estimated by turbidity measurements at different periods, is shown in Fig. 20.

In series 1 the best growth was in the first eight cultures which showed little difference during the first 10 days (Fig. 20, *A*). There was a noticeable inhibiting effect in the last two cultures, but as usual it subsequently became less and less marked (Fig. 20, *C*). In series 2 cultures 2–10 showed equally good growth during the first 2 weeks (Fig. 20, *B*), while in culture 1 the effect of phosphorus deficiency was noticeable.

The range of phosphorus concentration for an optimum growth of *Nitzschia palea* in series 1 is therefore about 0·018–1·78 p.p.m., while in series 2 it is about 0·018–8·9 p.p.m. or perhaps even higher, as no higher concentrations were used in this series. The lower limit of the optimum range is evidently lower than that (about 0·089 p.p.m.) for the other organisms so far studied. A good growth of *N. palea* was obtained in phosphorus concentrations of 0·018 p.p.m. in both series, though half that concentration (culture 1 of series 2) showed a deficient growth. The phosphorus concentration in many natural waters is very often within this optimum range (Chu, 1942, Table 7, p. 304), so that the growth of this diatom will be less frequently affected by a phosphorus deficiency than that of most other organisms. In the English lakes, however, the phosphorus concentration is generally below the optimum range for the growth of *N. palea* (cf. Pearsall, 1930).

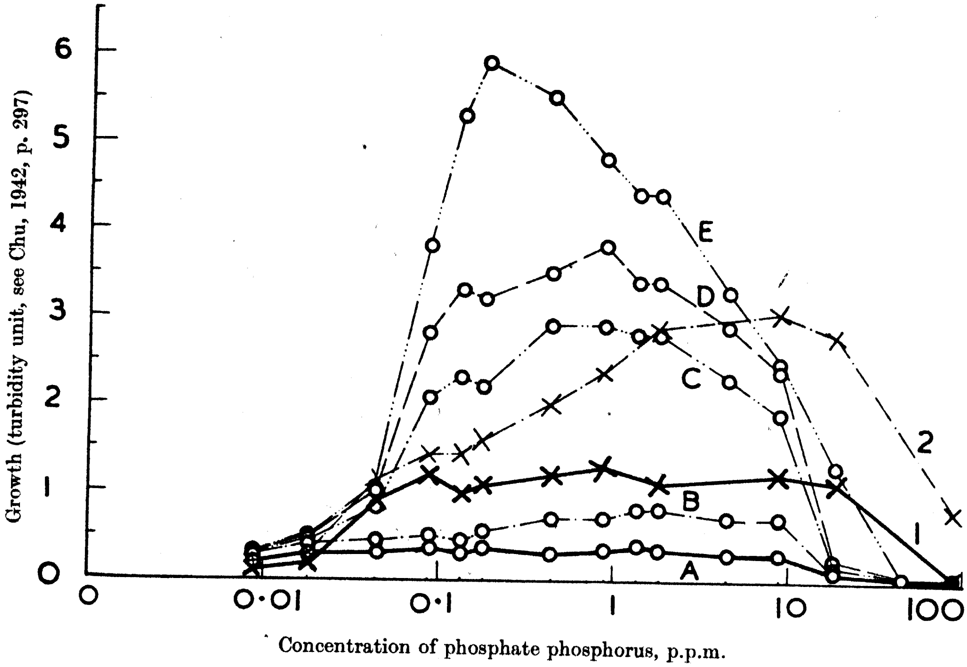

Fig. 21. Growth of *Tabellaria flocculosa* and *Asterionella gracillima* in different concentrations of phosphate phosphorus, expressed as turbidity: *A, B, C, D* and *E*, growth in one set of cultures of *Tabellaria flocculosa* (medium 10, Exp. 33) in 32, 44, 70, 83 and 138 days respectively; 1 and 2, growth in one set of cultures of *Asterionella gracillima* (medium 9, Exp. 9) in 45 and 70 days respectively.

(*e*) **Tabellaria flocculosa** Kütz.

Exp. 33. Medium 10, with $FeCl_3$ 1 p.p.m. and K_2HOP_4 varying from 0·05 to 500 p.p.m. in duplicate sets of fifteen 50 c.c. cultures, the phosphorus content being (1) 0·0089, (2) 0·018, (3) 0·045, (4) 0·089, (5) 0·13, (6) 0·18, (7) 0·45, (8) 0·89, (9) 1·34, (10) 1·78, (11) 4·45, (12) 8·9, (13) 17·8, (14) 44·5 and (15) 89 p.p.m.; illuminated 7 hr. daily in apparatus C; inoculum approximately 120 cells per c.c. of solution. The relative growth in cultures with different phosphorus concentrations in one set, as estimated by turbidity measurements at different periods, is shown in Fig. 21, *A–E*.

During the first 32 days the greatest growth was in cultures 2–12, and there was not much difference between them. That in culture 1 was poorer and showed the effect of phosphorus deficiency from the beginning, while in culture 13 there was a marked inhibiting effect, though the effect slightly decreased at a later stage. In the last two cultures there was no growth at all, and the high phosphorus concentration in the last culture was evidently fatal. The range of phosphorus concentrations affording an optimum growth for *Tabellaria flocculosa* is therefore approximately from 0·018 to 8·9 p.p.m., though there seems to be a slight initial set-back in concentrations of 4·45–8·9 p.p.m. There was a noticeable effect of phosphorus deficiency in a concentration of 0·0089 p.p.m. and a serious inhibiting effect in a concentration of 17·8 p.p.m. which will support an optimum growth of *Botryococcus*, *Pediastrum*, and *Staurastrum paradoxum*, when nitrate is the source of nitrogen in the medium. It is evident that *Tabellaria flocculosa* is less tolerant of high phosphorus concentrations than some other organisms. The growth rate in cultures 2–5 decreased successively during later periods in the usual way.

A striking feature of this experiment was the increased yellowing in later periods in cultures with higher phosphorus concentrations. This is the cause of the fall in the turbidity estimation of growth in cultures 11 and 12 after 10 weeks (Fig. 21, *C*), in 9–12 after 83 days (Fig. 21, *D*) and in 7–12 after 138 days (Fig. 21, *E*). During the fifth month culture 6 was still yellowish green, while in cultures 7–9 the green colour was less marked, culture 10 was whitish yellow, and cultures 11 and 12 were whitish. Culture 13 was of a pale colour during the whole period of the experiment. The decrease in the green colour component must, as in *Botryococcus*, be due to the higher concentrations of phosphorus which result in an absorption of more phosphorus and hence of proportionally less nitrogen as well as in a more intensified decrease of nitrogen in the solution in later stages as a result of its consumption during the preceding more rapid growth.

The upper limit of the optimum range of phosphorus concentration for *Tabellaria flocculosa* is lower than that for some other organisms, but is still beyond the phosphorus range occurring in ordinary waters. It is therefore unlikely that its growth in nature will be unfavourably affected by too high a phosphorus concentration. The lower limit of the optimum range, as in the case of *Nitzschia palea*, is lower than that for the other organisms studied, and within the range frequently found in a number of waters. There should therefore be less chance for the growth of these two diatoms in nature to be limited by phosphorus deficiency. This may be one of the factors accounting for the constant occurrence of *Tabellaria flocculosa* in the English lakes (Pearsall & Pearsall, 1925, pp. 61 and 65). In Windermere, during the summer of 1941, it was most abundant in the middle of the reed swamps where the concentrations of nitrogen, phosphorus and iron were much higher than in other parts of the lake.

(*f*) **Asterionella gracillima** (Hantzsch) Heiberg

Exp. 34. Medium 9, with K_2HPO_4 varying from 0·05 to 500 p.p.m. in four sets of twelve 10 c.c. cultures, the phosphorus contents being (1) 0·0089, (2) 0·018, (3) 0·045, (4) 0·089, (5) 0·13, (6) 0·18, (7) 0·45, (8) 0·89, (9) 1·78, (10) 8·9, (11) 17·8 and (12) 89 p.p.m.; illuminated for 7 hr. daily in apparatus C; inoculum approximately 166 cells per c.c. of solution. The relative growths of one set of cultures, as estimated by turbidity measurements, are shown in Fig. 21, 1 and 2.

The growth during the first 7 weeks was about equally good in cultures 3–11 (Fig. 21, 1), though culture 3 was slightly inferior in two sets. At the end of 10 weeks (Fig. 21, 2) only cultures 9–11 continued to grow well. There was no marked yellowing in higher phosphorus concentrations during the later periods, such as occurred in the cultures of *Tabellaria flocculosa.* The optimum range of phosphorus concentration for *Asterionella gracillima* is therefore about 0·045–17·8 p.p.m. Phosphorus deficiency was shown in the lower concentrations and a marked inhibiting effect in the higher ones.

There is a considerable difference in the effect of high phosphorus concentrations on the growth of *Asterionella gracillima* and of *Tabellaria flocculosa.* A phosphorus concentration of 17·8 p.p.m. exerts a serious inhibiting influence on the growth of the latter, but it is still within the optimum range for the former. The inhibiting effect of a phosphorus concentration of 89 p.p.m. on *Asterionella gracillima* is strong, but not as marked as that of 44·5 p.p.m. on *Tabellaria flocculosa,* since the effect decreases in later stages (cf. Fig. 21, *A–E* and 1 and 2). This difference will not affect the occurrence of these two diatoms in nature, as the phosphorus concentration of ordinary waters is generally much below 1·78 p.p.m. On the other hand, *Asterionella* seems less able to utilize phosphorus in so low a concentration as 0·018 p.p.m. (probably also in lower concentrations) than *Tabellaria.* Optimum growth of the latter was obtained in concentrations of 0·018 p.p.m. in which *Asterionella* cultures show the effects of phosphorus deficiency.

In the English lakes the phosphorus concentration is always below the optimum range for the growth of *Asterionella,* so that fluctuations in the phosphorus content of the water should have a great effect on its growth. Pearsall (1932) found that the occurrence of *Asterionella* was correlated with phosphate concentration, particularly in Ullswater. There also seems to be a striking correlation in other lakes, where the general conditions were suitable for its growth. Fig. 22 is plotted from Pearsall's (1930, 1932) chemical analyses and plankton estimations (as percentages) in Windermere, Lake Esthwaite, Bassenthwaite, Derwentwater and Ullswater which are the only lakes with a prominent growth of *Asterionella.* The scarcity of *Asterionella* in other lakes is due either to lack of calcium (Pearsall, 1932, p. 246) and nitrogen (Ennerdale and Wastwater) or to the general conditions being more suitable for the growth of other organisms (Crummock and Lowes Water). The correlation is closest in Windermere and Lake Esthwaite (Fig. 22, *D*, *E*), where *Asterionella* was a dominant form. The discrepancy in Ullswater and Derwentwater during March (Fig. 22, *A*, *C*), when the *Asterionella* growth was poor at a time when the phosphate content was the highest of the year, must be due to the abundant growth of *Tabellaria fenestrata.* As pointed out above (p. 172), the increase and decrease of *Asterionella,* particularly in Derwentwater, Bassenthwaite and Ullswater, is also influenced by the rise and fall in the nitrogen concentration of the water.

(*g*) *General consideration of the influence of phosphorus concentrations on the growth of the organisms studied*

On the whole, although there are minor differences, the various algae investigated react in a similar way to variations in phosphorus concentrations. The lower limit of phosphorus concentration, admitting of optimum growth, is approximately from 0·018 to 0·098 p.p.m., and the rate of growth is not much affected by an increase of phosphorus concentration up to the highest limits that have been recorded in ordinary fresh waters. In nature, therefore, no unfavourable effect of high phosphorus concentrations is to be expected, and the algae studied will be independent of the rise and fall of phosphorus concentration as long as it remains above the lower limit for optimum growth.

The upper limit of phosphorus concentration for optimum growth, though nearly always beyond the range occurring in natural waters, differs slightly for the different organisms and varies according to the composition of the solution. No marked inhibiting effect has ever occurred in phosphorus concentrations less than 8·9 p.p.m., while a concentration of more than 17·8 p.p.m. always exerts a marked arresting effect on the growth of all the organisms studied. The source of nitrogen seems to influence the inhibiting effect in high phosphorus concentrations. Generally speaking, the upper limit of phosphorus concentrations for optimum growth is always higher when nitrate is supplied than when an ammonium salt is supplied. Thus the inhibiting effect on *Pediastrum*, *Staurastrum* and *Nitzschia* becomes pronounced at a phosphorus concentration of 8·9 p.p.m. in a medium containing ammonium as the only source of nitrogen, while there is no inhibiting effect at the same phosphorus concentration in media with KNO_3 or $Ca(NO_3)_2$ as the source of nitrogen. In such media a distinct inhibiting effect only occurs in cultures with a phosphorus concentration not less than 17·8 p.p.m. In cultures of the diatom *Tabellaria flocculosa*, supplied with nitrate, there is an evident inhibiting

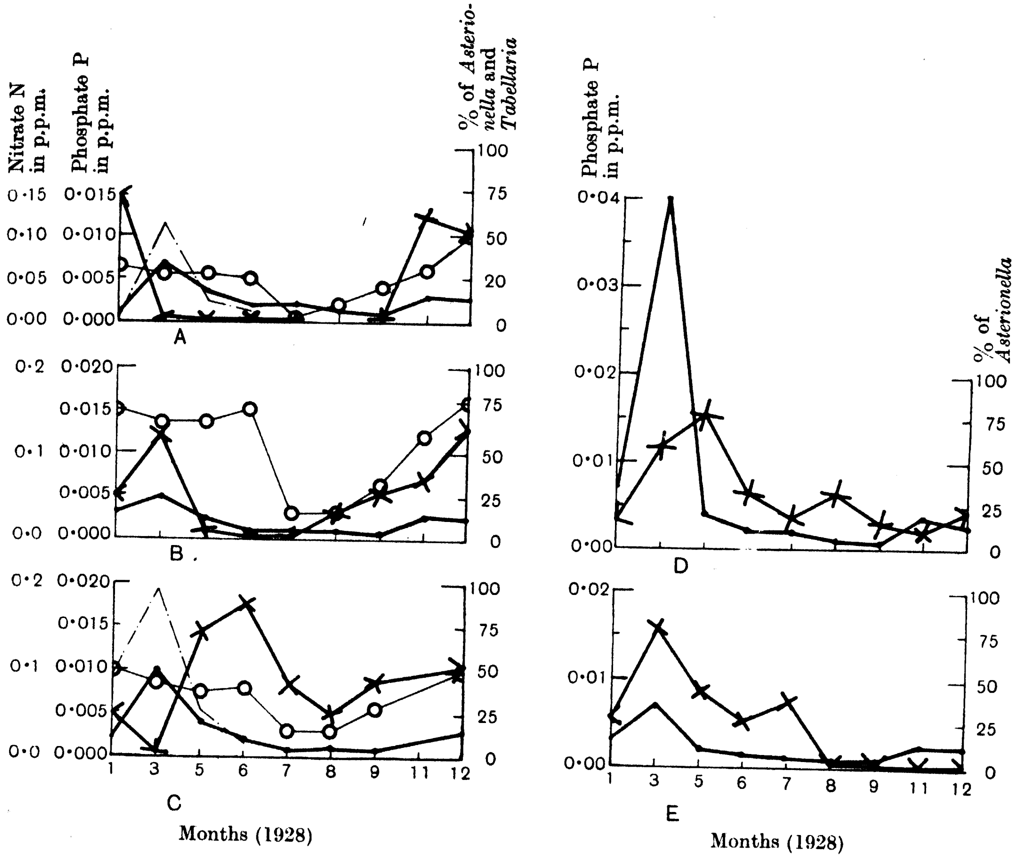

Fig. 22. Correlation of the growth of *Asterionella gracillima* with the phosphorus concentration in the English lakes during 1928, plotted using Pearsall's (1930, 1932) data: *A*, Derwentwater; *B*, Bassenthwaite; *C*, Ullswater; *D*, Windermere; and *E*, Esthwaite Water. ——•——•—— Phosphate phosphorus; —×—×— *Asterionella*; —o—o— Nitrate nitrogen; —·—·— *Tabellaria fenestrata*. (Only the percentages during January to June are plotted for the sake of clearness.)

effect in a phosphorus concentration of 17·8 p.p.m. which supports an optimum growth of *Pediastrum boryanum*, *Staurastrum paradoxum*, *Botryococcus*, *Asterionella* and possibly also of *Nitzschia palea*.

For ordinary purposes 5 p.p.m. of K_2HPO_4 furnishes sufficient phosphorus to admit of growth over a considerable period, though the length of this period varies with different forms. For short-term cultures 1 or 2 p.p.m. of K_2HPO_4 admit of the utilization of a nitrogen concentration of about 5 p.p.m. by most of the planktonts so far cultured. With such a nitrogen concentration supplied as nitrate an increase of phosphorus, though harmless if it does not exceed 8·9 or 17·8 p.p.m. is not of much value, since nitrogen deficiency becomes a limiting factor before the phosphorus concentration falls below the lower optimum limit. In the media hitherto used for culturing algae the amount of phosphate is often too high, since it generally varies between 0·05 and 0·5 g. per litre (see Kufferath, 1929; Bold, 1942), giving a phosphorus concentration of 9–110 p.p.m. Such concentrations are mostly beyond the general optimum range for most planktonts, and will exert an inhibiting effect, which will become very marked when the phosphorus exceeds 18 p.p.m. This is evidently one reason for the usual failure to obtain thriving cultures with such media.

This fact will have to be taken into consideration in the artificial fertilization of fish ponds. It will be necessary to ensure that the concentration of soluble phosphorus is not so high as to lower the rate of multiplication of the phytoplankton. The phosphorus concentration should be kept at about 0·2–2·0 p.p.m., and frequent addition of small amounts of fertilizer rather than the use of a large quantity at a time is advisable.

When the phosphorus concentration is below the lower optimum limit, it has a definite limiting effect on the phytoplankton if other factors are not already operating. This lower limit for *Asterionella* is about 0·045 p.p.m., and for the other two diatoms, 0·018 p.p.m., while for the other organisms it is 0·089 p.p.m. There is a progressive decrease in the rate of multiplication the more the phosphorus concentration falls below these limits. A slight rise or fall in the phosphorus concentration at this level will markedly influence the development of the algae studied, and the lower the concentration the more marked will be the effect of a rise or fall.

Generally speaking, given sufficient available nitrogen, sunshine, and silica, a limiting effect on phytoplanktonts due to phosphorus deficiency will occur at certain times in nearly all natural waters (cf. Chu, 1942, p. 304, Table 7). The failure of certain investigators to observe such an effect must, as previously indicated, be due to other limiting factors having come into operation before a state of deficiency arose.

In cultures with phosphorus concentrations within the limits of the optimum range, growth is always uniform, until a state of phosphorus deficiency arises when the growth rate becomes slower and slower. Optimum growth therefore shifts to cultures with higher and higher initial concentrations as an experiment proceeds, until growth is limited by lack of nitrogen (see Figs. 17–19). This progressive change is much slower and less marked than in Exps. 18–26 with varying nitrogen concentrations (see Figs. 9–14), since the consumption of phosphorus as a whole is much slower than that of nitrogen.

Gardiner (1941*a*) has shown that the growth of diatoms in a reservoir ceases when the phosphorus concentration falls to a low level, though he believes that 'there is unlikely to be a direct causal connexion between cessation of the first growth and reduction in silicon and phosphorus concentrations'. Fig. 23 is plotted from the monthly average of diatom growth and phosphorus concentration in Gardiner's Table 1, and the concentration of nitrate nitrogen in the same reservoir during 1938 (Metropolitan Water Board, 33*rd Ann. Rep.*). The effect of different phosphorus concentrations on the development of all the dominant diatoms in the waters studied by Gardiner has not been tested by experiment. There is unlikely to be any great error, however, if it is assumed that the lower limit of optimum phosphorus concentration is somewhat between 0·02 and 0·09 p.p.m., since most of the organisms investigated by me have their lower optimum limit in this region. On this assumption it is evident that the diatom crop remains considerable, as long as the phosphorus concentration is above this lower limit, no matter how large the actual variation in amount (Fig. 23, Jan. to May 1939). As soon, however, as the concentration falls to about 0·006 p.p.m. (May, isolated point '*a*'), there follows a sudden decrease in the diatom population, which is checked when the phosphorus concentration rises to about the lower optimum limit a week later. The long-continued minimum shown by the diatom plankton at a time when the phosphorus concentration had increased to above the lower optimum limit must, as in the preceding year (Fig. 23, May to August, see also p. 172), be due to the limiting effect of nitrogen deficiency which always occurs during summer in this reservoir (see Metropolitan Water Board, 30*th to* 33*rd Ann. Rep.*); no data as to the nitrogen content in 1939 are at present available. The decrease of the diatom crop from March to May of 1938 must be due partly to the fall in nitrogen and partly due to the fall in phosphorus concentration, though Gardiner is of the opinion that it

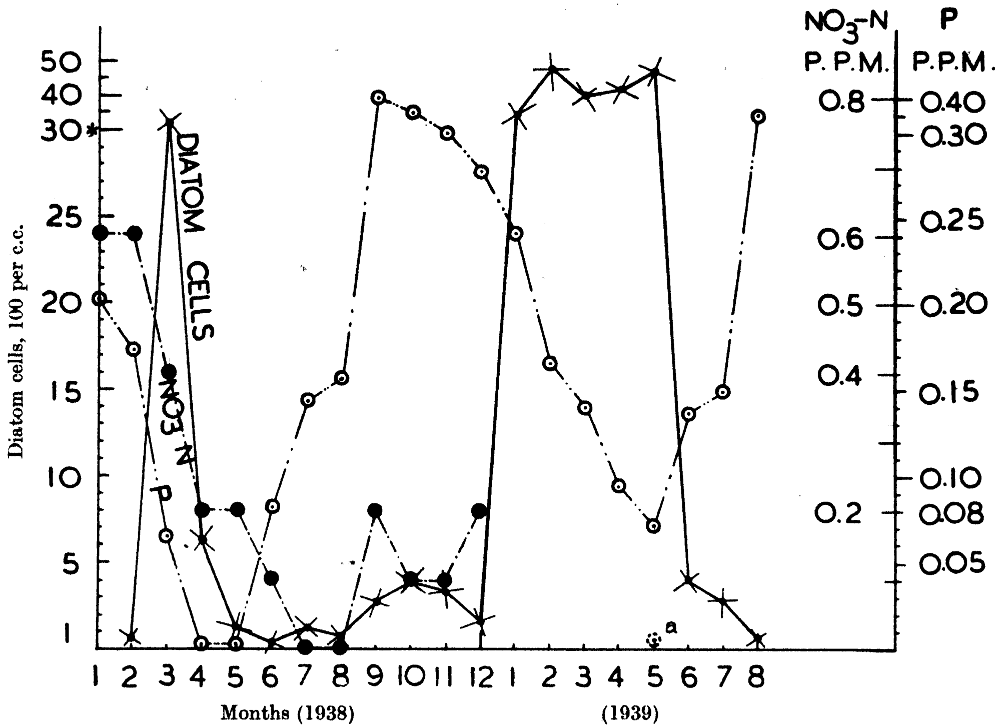

Fig. 23. Monthly variations in the number of diatom cells and the amounts of nitrate nitrogen and soluble phosphorus in the Barn Elms No. 8 Reservoir, based on the data of Gardiner (1941 *a*) and Metropolitan Water Board (33*rd Ann. Rep.*). * Change of scale.

'is not due to the exhaustion of the available supplies of silicon or phosphorus'. He suggested that 'the termination of the period of rapid multiplication of one or another species of diatom may very well be due either to the exhaustion of some other plant nutriment or to a disturbance of the ratio of certain essential ions, for instance the nitrogen : phosphorus ratio'. The latter possibility is not very likely, as my experiments show that the growth of planktonts is not markedly affected by an increase or decrease of nitrogen or of phosphorus and is independent of the N/P ratio in the solution, as long as these elements remain in optimum concentration. It is mainly the deficiency of nitrogen or phosphorus, but not the N/P ratio, that limits the growth of the planktonts studied, when the concentrations of these elements are below the optimum range. The effect of the N/P ratio on the growth of planktonic organisms was dealt with elsewhere (Chu, 1941, p. 149).

III. Summary and conclusions

1. The influence of the nitrogen and phosphorus concentrations in the medium on the growth of *Pediastrum boryanum*, *Staurastrum paradoxum*, *Botryococcus Braunii*, *Nitzschia palea*, *Fragilaria crotonensis*, *Tabellaria flocculosa* and *Asterionella gracillima* are investigated, using media synthesized with pure inorganic chemicals as described in Part I (Chu, 1942). The range of concentrations used in the experiments generally includes that found in natural waters. The bearing of the experimental results on the occurrence of planktonic organisms in nature is discussed in relation to the nitrogen and phosphorus concentrations observed in fresh waters.

2. The upper limits of concentrations of nitrogen and phosphorus for optimum growth of the plankton organisms studied are always higher than the highest concentrations occurring in ordinary waters, so that their growth is unlikely ever to be unfavourably affected by too high a concentration of nitrogen or phosphorus. On the other hand, the concentrations of nitrogen and phosphorus in nearly all natural waters frequently fall below, or in some never reach, the lower limit for an optimum growth, so that, when other conditions are suitable for growth, a limiting effect due to deficiency of these elements may be expected everywhere during certain periods of the year.

3. The lower limit of the optimum range of nitrogen concentration differs for different organisms. It generally varies approximately from 0·3 (*Fragilaria crotonensis*) to 1·3 (*Pediastrum boryanum*, *Nitzschia palea*) and sometimes to 2·6 or 5·3 (*Staurastrum paradoxum*) p.p.m., when an ammonium salt is the source of nitrogen; and from 0·3 (*Botryococcus Braunii*) to 0·9 (*Staurastrum paradoxum*) p.p.m. when nitrate is the source of nitrogen. Below these limits the growth rate decreases with decreasing concentration of nitrogen. In nature a low nitrogen concentration may have a slightly different effect on different planktonts. For example, a nitrate nitrogen concentration of about 0·4 p.p.m., which is suitable for the growth of *Botryococcus*, may limit that of *Pediastrum boryanum* (lower limit of optimum range about 0·7 p.p.m.) and *Staurastrum paradoxum*, if the amount of ammoniacal nitrogen in the water is less than 0·1 p.p.m.

4. The upper limit of the optimum range of nitrogen concentration varies approximately from 5·3 (*Staurastrum paradoxum*) to 13 (*Pediastrum boryanum*, *Fragilaria crotonensis*) p.p.m. when an ammonium salt is the source of nitrogen, and from 3·5 or 7·0 (*Botryococcus*) to 17 (*Asterionella*) p.p.m. when nitrate is the source of nitrogen. Beyond these limits there is an increasing inhibiting effect.

5. Optimum growth of all the organisms studied can be obtained in nitrate-nitrogen concentrations from 0·9 to 3·5 p.p.m. and phosphorus concentrations from 0·09 to 1·8 p.p.m., while a limiting effect on all of them will occur in nitrogen concentrations from 0·1 p.p.m. downwards and in phosphorus concentrations from 0·009 p.p.m. downwards, and marked inhibiting effect will occur in concentrations of nitrogen or phosphorus from 45 p.p.m. upwards.

6. Nitrogen in the form of ammonia can be directly utilized by the algae studied. The optimum range of nitrogen supplied in this form may differ from the optimum range of nitrate nitrogen, especially as regards the lower limits which are often lower for nitrates. The nature of the nitrogen supply also affects the optimum range of phosphorus concentrations, the upper limit of which is often much lower when nitrogen is provided as ammonium salt than when nitrate is used.

7. The lower limit of the optimum range of phosphorus concentration varies from about 0·018 (*Nitzschia palea, Tabellaria flocculosa*) to about 0·09 (*Pediastrum, Staurastrum paradoxum, Botryococcus*) p.p.m.; and the upper limit from 8·9 (*Nitzschia palea, Tabellaria flocculosa*) to 17·8 (*Pediastrum, Staurastrum paradoxum, Botryococcus*) p.p.m. when nitrate is the source of nitrogen, while it lies at about 1·78 for all the planktonts studied when ammonium is the source of nitrogen. Low phosphorus concentrations may, therefore, like low nitrogen concentrations, exert a selective limiting influence on a phytoplankton population; for example, a phosphorus concentration of 0·02 p.p.m., which has no limiting effect on the growth of *Nitzschia palea* and *Tabellaria flocculosa*, may be insufficient for the optimum growth of others.

8. No increase or decrease in the concentration of nitrogen or phosphorus, and no change in the value of the N/P ratio can markedly affect the growth of any of the organisms studied, so long as these elements remain within the optimum range for the growth of the organism in question.

9. The nitrogen concentration determines to a large extent the amount of chlorophyll formed. A yellowing or whitening effect always occurs in nitrogen-deficient cultures. Phosphorus deficiency also produces a yellowing effect. Nitrogen concentrations beyond the optimum range inhibit the formation of chlorophyll in green algae.

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THE VEGETATION OF THE KARAMOJA DISTRICT, UGANDA

AN ILLUSTRATION OF BIOLOGICAL FACTORS IN TROPICAL ECOLOGY

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(*With Plates* 3–11 *and one Figure in the Text*)

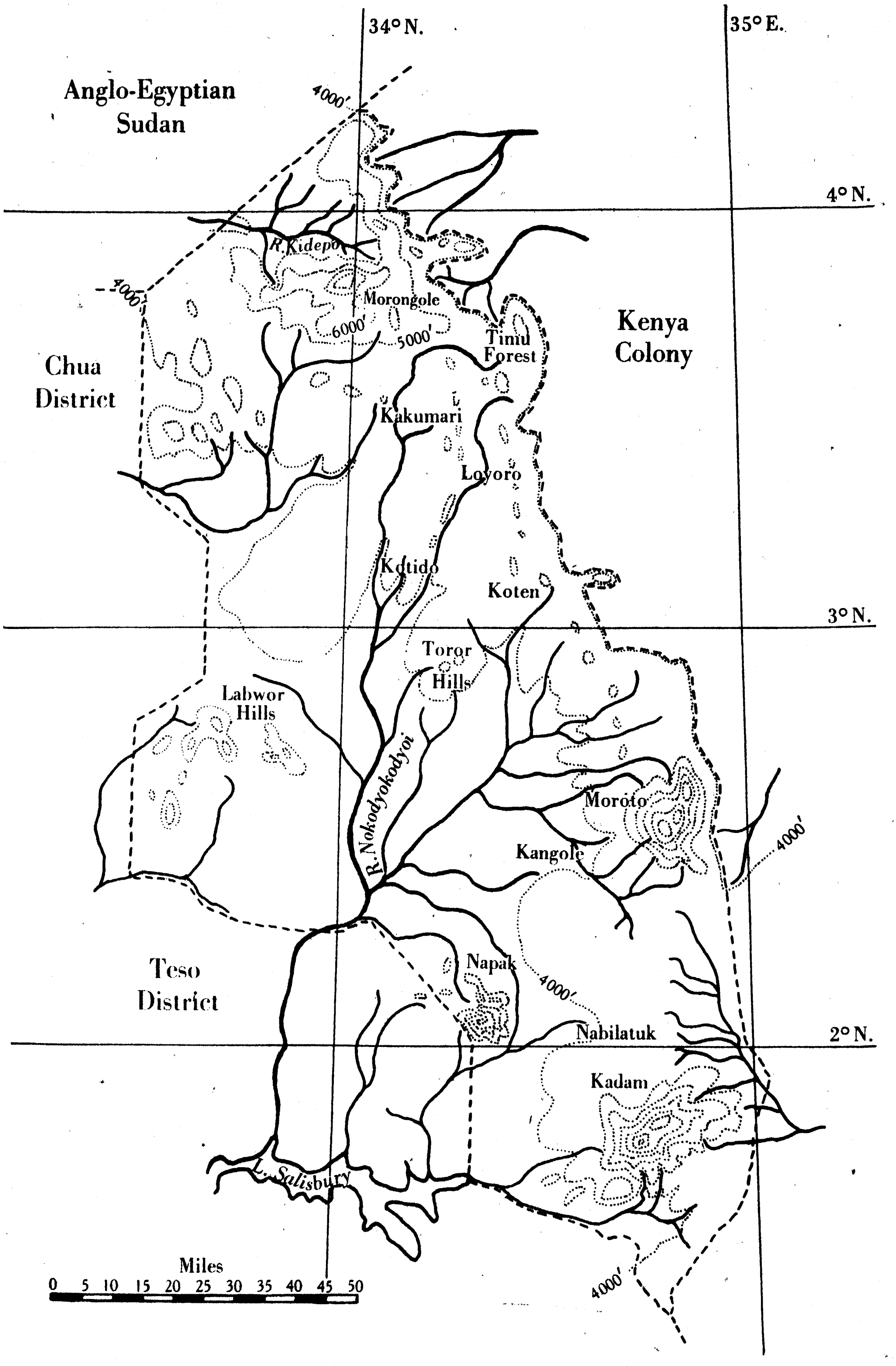
Introduction

The district of Karamoja is situated in the north-east of the Uganda Protectorate; on the north it is bordered by the Anglo-Egyptian Sudan, and on the east by Kenya Colony. Karamoja, which lies mostly between the parallels of latitude 1° 30′ and 4° N. and of longitude 33° 30′ and 35° E., has an area of over 11,000 sq. miles. The topography of Karamoja has been briefly described by Wayland & Brasnett (1938). The district consists essentially of a plain rising eastwards and northwards to the hilly land bordering the escarpment above the Turkana district of Kenya; some of the land in the south-west is below 1000 m., but most of the district lies above this altitude.

The rocks underlying most of Karamoja are those of the Basement Complex; towards the south-east of the district are many tertiary volcanic piles, the largest being Kadam (Debasien) 3200 m., Napak (Kamalinga) 2500 m., and Moroto 3050 m.; in the north there are rugged hills, composed of Basement Complex rocks, culminating in Morongole at an altitude of 2600 m.

Numerous streams and rivers rise in the hills and mountains on the east of Karamoja and flow towards the south and west. The slopes of the mountains are often steep, and after storms the rivers come down in spate over their rocky beds. When the rivers reach the plains their character changes and they flow in deep wide channels, filled with water after storms in the hills, but dry for the greater part of the year. Even when there is no visible flow of water, however, there is drainage along the deep sandy beds of these watercourses; holes are dug in them to provide water for men and stock. On the plains in the west, the river channels become less defined, opening out into wide shallow depressions, swampy during the rains but dry for the greater part of the year.

Karamoja is the driest district in Uganda. The only long series of rainfall records available are those from Moroto station, where the average precipitation over a period of 19 years has been 90 cm. The records show great variation from year to year: in 1937 the rainfall was 148 cm., in 1924 it was only 48 cm. Inspection of the records for the last 5 years shows that in this period, however, there were only 12 months in which less than 1 cm. of rain fell, and that only on two occasions were two such dry months in succession. December and January are usually the driest months, and the wettest are usually April and May. The effectiveness of the rainfall is much diminished by the fact that a large proportion of it is in the form of torrential downpours. The only humidity figures available are those from Moroto, and these do not apply to the district as a whole, for the station is situated in a sheltered valley facing west and is not exposed to the hot dry east winds which sweep across the plains of Karamoja throughout most of the year. Moroto station


34° N.
35° E.
Anglo-Egyptian
Sudan
4000'
4° N.
R. Kidepo
4000'
Morongole
6000'
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Timu
Forest
Kenya
Colony
Chua
District
Kakumari
Loyoro
Kotido
Koten
3° N.
Toror
Hills
Labwor
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R. Nokodyokodyoi
Moroto
4000'
Kangole
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District
Napak
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Nabilatuk
2° N.
Kadam
L. Salisbury
Miles
0 5 10 15 20 25 30 35 40 45 50
4000'

is at the base of the mountain of that name and it is certain that the rainfall out on the plains is much less: Wayland & Brasnett have suggested that it may amount to only about 25 cm. per annum.

The soils of Karamoja have been described by Martin in an appendix to the report by Wayland & Brasnett. The soils in the plains and valleys of the district consist of dark grey or dark brown calcareous clays (often erroneously termed 'black cotton soil'), which are noteworthy for their extreme stickiness when wet and for their tendency to form large deep cracks when dry. These clays are derived both from wind and water deposits: on the banks of many of the rivers there may be seen profiles such as that one illustrated by Wayland & Brasnett's report, showing wind-blown fine sands interbedded between water-borne silts. The soils of the higher lands to the east of Karamoja are quite different from those of the plains; some of the steeper hills have a soil of comminuted rock fragments; on the lower hills the soil usually is a red-brown fine-grained loam.

Karamoja is the most sparsely populated district in Uganda: in 1931 the population numbered about 66,000 and there were only 6·1 people per sq. mile, while for the whole protectorate the figure was 44·2. Most of the inhabitants of Karamoja belong to a group of tribes, similar in habits and in language, known collectively as Karamojong. Small groups of other tribes are found—the so-called Wanderobo in the north, Dopeth on the mountains, and in the south-east there are several villages of Suk people. Formerly, all these tribes were in a state of strife against each other and against their neighbours, notably the Acholi to the west and the Turkana to the east; there are still frequent quarrels about supplies of water for stock.

The Karamojong are a pastoral people and, although the human population is small, the population of domestic animals is very large. The latest returns showed that there were about 400,000 cattle, 300,000 sheep, 400,000 goats and 36,000 donkeys in the district. The whole life of the people is centred around their stock, which furnish the main food supply, for the staple diet of the Karamojong is a curdled mixture of blood and milk. The permanent settlements consist of family groups living in large enclosures, fenced with thorny branches to protect the stock at night from lion, leopard and hyena, all of which are abundant in the district. These enclosures, which are known as 'manyattas', are situated in the east of the district, near permanent waterholes. Some of the waterholes have been dug as much as 8 m. deep, the water being passed up in large calabashes by a chain of women and girls, standing on steps on the side of the hole; in spite of the depth of the holes, many of them dry up and water supplies become scarce in the dry seasons.

Grazing also becomes very scarce in the east during the dry seasons, and therefore it has become a feature of tribal life that the men take much of the stock—especially the full-grown cattle—over to the west of the district early in the dry season and return to the east at the beginning of the rains. The lowlying grasslands of the west are very swampy during the rains and some areas are under water for short spells (in fact, one of these areas was shown on early maps of Uganda as permanent water under the name of Lake Kirkpatrick). There is an abundance of grazing on these western areas in the dry season, but it cannot be fully utilized, as waterholes are scarce and far apart.

The animals which remain in the east, cattle, sheep and goats, obtain a large proportion of their nourishment by browsing on trees and shrubs and, except during periods of prolonged drought, their condition is surprisingly good in spite of the shortage of grass. The Karamoja cattle are of a humped type with fairly short horns; in spite of the rigorous conditions under which they live, they are much larger in bone and much better in condition than the long-horned Ankole cattle in the south-west of Uganda, where abundant supplies of water and grazing are available. There is little doubt that the mineral status of the soils is a major factor in determining the condition of the cattle; the Karamoja soils are rich in lime, but most of the Ankole cattle are living in areas with acid soils containing little lime. Well-defined 'licks', sometimes at the base of anthills and sometimes near springs, are utilized by wild and domestic animals in the south-west of Uganda, but such licks are not noticeable in Karamoja; it is probable that normal grazing on the soils of the district amply supplies the mineral requirements of the animals.

Although the Karamojong are dependent mostly on their cattle for their food, yet they cultivate large areas of *Sorghum vulgare* Pers. near the rivers; the largest cultivations are those around Kangole, west of Moroto, and around Kotido, north of the Toror Hills; a large proportion of the grain is used to make beer, but some of it is eaten. Other foodstuffs are grown in smaller quantity and the diet is supplemented by the roots, leaves and fruits of many wild plants. There is some evidence that the Karamojong were cultivators before they assumed a pastoral habit, and it seems that before the Karamojong came into the district from the east, Karamoja was inhabited by an agricultural grain-eating tribe whose stone-hut circles and grindstones still remain, widely scattered.

Until fairly recently, little was known about the vegetation of Karamoja. In the first decade of the century, the district was not administered and was the scene of much raiding and ivory poaching. In 1911 a touring officer was appointed, but the district continued to be very unsettled for the next few years and the first civilian District Commissioner was appointed in 1919. The first important botanical collection made in the district was that of Liebenberg in 1931; since then Eggeling (in 1936), Brasnett (in 1937) and the author (in 1936, 1939 and 1940) have amassed considerable numbers of specimens, and it is possible to write a preliminary account of the vegetation. But the flora is by no means completely known, for it is difficult to travel through Karamoja in rainy weather, when the herbs are in active growth and, as many of the woody plants have a very short flowering period, it has not been possible to obtain material sufficient for specific determinations of all of them.

THE PLANT COMMUNITIES OF KARAMOJA

The vegetation of Karamoja may be discussed conveniently by considering the plant communities in the following order, proceeding from the south and west towards the north and east. The terms used to describe the types are (with slight modifications) those postulated by the Vegetation Committee of the East African Pasture Research Conference (1940). This committee endeavoured to draw up a scheme whereby East African vegetation would be classified according to its life form, without the use of any local or imported vernacular words. Under this classification the main types of Karamoja classification are as follows; for convenience, there are shown in brackets the corresponding terms suggested by Burtt Davy (1938):

(1) Open grasslands of the plains in the south and west (grass-steppes).
(2) Woodlands of the hills in the south and west (tropical savanna-woodlands).
(3) Grasslands of the broad valleys in the centre (marsh-grasslands).
(4) Cultivated land in the east.
(5) Grasslands in the east (grass-steppes and savannas).

(6) Riverain forests (tropical riverain forests).

(7) Woodlands in the east and north (tropical savanna-woodlands).

(8) Acacia woodlands and thickets in the east (tropical thornland).

(9) Mountain vegetation—woodlands, forests, shrubby moorlands, grass moorlands (tropical savanna-woodlands, tropical upper-mountain rain forest, tropical alpine elfin-woodland, mountain grassland).

(1) *Open grasslands of the plains in the south and west*

These plains are of dark grey calcareous clay ('black cotton soil') which becomes tenacious and impermeable when wet. In consequence, large areas are waterlogged and even flooded for considerable periods in the wet season; with the advent of dry weather, they dry up and crack deeply. In some localities there are no permanent waterholes and therefore the grasslands cannot be used much for grazing—they are too swampy in the wet seasons and no water supplies are available in the dry seasons. These ungrazed areas have a characteristic blue-green colour when viewed from a distance in wet weather; the colour is due to the glaucous foliage of *Hyparrhenia dissoluta* C. E. H., the dominant species of grass. A distant view will give an impression of a close cover of fairly short grass, but closer inspection will show that the grass is tall (up to 2½ m. high) and relatively sparse, for there is much bare soil between the small tufts of erect stems.

Permanent waterholes are to be found in some places, for example, to the north of Napak and to the south of the Labwor Hills, and there is intensive grazing around these waterholes during the dry seasons. Where this grazing occurs, the grass is shorter than in ungrazed parts, attaining a height of about 1½ m., and it contains a mixture of species (Pl. 3, phot. 1). *Hyparrhenia dissoluta* is one of the constituents of these grazed areas, but it is not the dominant species; in some areas *Hyparrhenia rufa* Stapf is dominant and in others *Hyparrhenia filipendula* Stapf. Most of the moderately grazed well-drained grasslands also include several other species, notably *Themeda triandra* Forsk., *Setaria sphacelata* Stapf & Hubb., *Cymbopogon excavatus* Stapf and *Andropogon gayanus* Kunth. var. *squamulatus* Stapf. In places where the grazing has been more intense, for example on the low hill Opopwa, north of Napak, the cover of grass is shorter, being less than 1 m. high in the rains; *Themeda triandra* is dominant, *Brachiaria brizantha* Stapf and *Sporobolus pyramidalis* P. Beauv. are abundant, and much bare ground is exposed.

In the hollows where grazing has been fairly intense, a different type of grassland is found, in which *Setaria* spp. are dominant; this type is discussed under the heading '(3) Grasslands of the broad valleys'.

(2) *Woodlands of the hills in the south and west*

The dark clay soils of the plains give place to browner and redder loams on the lands which are not flooded for any considerable part of the year; on the lower slopes of many of the hills, at an altitude of about 1000 m., these loams are underlain by lateritic ironstone pavements. In some places, for example on Opopwa Hill, these higher lands are covered with open grassland, but in other localities trees are common in the grassland and, near the base of the Labwor Hills and Napak, the trees are dense enough to form a woodland. (It is hoped that the term 'woodland' will replace 'savannah forest' in East African ecology, for the woodland is neither a savannah—of which the original meaning was a treeless plain—nor a forest.)

The most common tree species are *Combretum binderianum* Kotsch., which is abundant even in some places which are swampy for short spells during the rains, *C. gueinzii* Sond. which is common on higher land, *Bauhinia thonningii* Schum., *Lonchocarpus laxiflorus* Guill. & Perr., *Gymnosporia senegalensis* Loes., *Strychnos inocua* Del., *Terminalia spekei* Rolfe, *T. velutina* Rolfe (Pl. 3, phot. 2). Most of these species are small, up to about 8 m. in height, and the majority of them are deciduous; this deciduous habit, together with their thick bark, enables them to withstand the fires which annually sweep through these woodlands. The trees are spaced fairly widely apart, and below them there is a dense growth of grasses, together with a few other herbs, whose height varies from about 1½ to 2 m.; as in the open grassland, so also in the woodland, the more intense the grazing, the shorter the height of the grasses. The same grass species as occur in the open grasslands occur also in the woodlands—*Hyparrhenia dissoluta*, *H. filipendula*, *H. rufa*, *Setaria sphacelata* and *Themeda triandra* are all common; an additional species is *Panicum maximum* Jacq., which is frequent in the shade of the trees.

The Labwor Hills, which rise to a height of about 1900 m. near the west of the district, are covered with woodland up to the summits where large masses of gneiss are exposed. Some of the species common on these hills are not reported from the mountains of eastern Karamoja, notably *Sterculia cinerea* A. Rich., *Oxytenanthera abyssinica* Munro, and *Vellozia* sp. which is locally abundant on big exposed masses of rock (Pl. 4, phot. 3).

(3) *Grasslands of the broad valleys in the centre of the district*

Between the four groups of hills—Toror, Moroto, Napak and Labwor—there lies a wide depression of land which to a distant view seems almost level, but which in fact is composed of broad shallow valleys and low ridges. During the rains many streams flow from the north and east into this depression; there is a certain amount of drainage out of this system into Lake Salisbury, but much of the water is retained and many of the lower parts are waterlogged and even flooded during wet spells. The soil is dark calcareous clay which is so tenacious that it is difficult to walk through it when wet: in dry seasons the ground becomes hard and cracks deeply. Such grasslands, waterlogged at some seasons and dry at others, are extensive in East Africa, but no simple term to describe them has yet been evolved; 'Inundation Plain Grassland' has been suggested; they have been described by Michelmore (1939) and Burtt (1942) under the vernacular name of 'mbuga'.

Large stretches of open grassland are found in this region, especially to the west of it, in the valley of the River Nokodyokodyoi and its tributaries. This grassland consists of large clumps of grass about 1½ m. high, widely spaced, with a considerable amount of bare exposed ground between the tussocks. In this area the dominant grasses are *Setaria holstii* Herm. and *S. incrassata* Hack.; *Panicum meyerianum* Nees, *P. porphyrrhizos* Steud., *Eremochloa haploclada* Stapf and *Dicanthium annulatum* Stapf are common. A few other herbs are common—notably *Clitoria ternatea* L., *Tragia hildebrandtii* Muell-Arg., *Euphorbia systyloides* Pax. and *E. hypericifolia* L.

The grasslands in many of the valleys, such as that of the River Nokodyokodyoi, are not heavily grazed for they are too wet in the rainy seasons and there are no permanent waterholes in the dry seasons. There are waterholes towards the east, and for miles around them grazing has been carried on. These pastures are shorter and contain a larger proportion of *Pennisetum ramosum* Schweinf.; in many areas it is the dominant grass. On slightly higher ground, less subject to waterlogging, other grass species—*Themeda triandra*, *Setaria* *sphacelata* and *Sporobolus pyramidalis*—are abundant; there is no sharp division between the swampy grasslands and the drier grasslands described above, for the two communities merge one into the other.

Many of the lower stretches of grassland in the east of this area contain numerous scattered specimens of gall acacia, *Acacia drepanolobium* Harms., which grows into a stunted small tree, about 3 m. in height (Pl. 4, phot. 4). Near the rivers are strips of acacia woodland consisting of *A. seyal* Del. and *A. seyal* var. *fistula* Oliv., growing to a height of about 15 m. (Pl. 5, phot. 5); although the trees are closely spaced in some places, yet they do not cast a dense shade and there is a fairly dense growth of grasses, notably *Setaria incrassata, Themeda triandra* and *Hyparrhenia* spp., beneath them.

The nearer to the settlements in the east with permanent supplies of water and a permanent population of men and domestic animals, the more intense the grazing. The tufts of grass become smaller and sparser, for only species which are resistant to very hard grazing can survive; *Pennisetum ramosum*, whose basal shoots are woody and unpalatable, is the most important of these. In the neighbourhood of Kangole there are large stretches of land on which even this species is scarce; such areas are bare for the greater part of the year, but for a short spell during the rains they are vivid green with a low covering of herbs and subshrubs, the most abundant plants being *Abutilon guineense* Bak. f. & Exell., *Triumphetta flavescens* Hochst., *Ipomea mombassana* Vatke., and *Commelina kotschyi* Hassk.; occasional specimens of grasses are to be seen—*Cynodon plectostachyum* Pilg., *Lintonia nutans* Stapf, *Panicum meyerianum* and *Pennisetum ramosum*, but the total amount of grass species does not cover one per cent of the ground.

(4) *Cultivated land in the east*

Large areas are cultivated each year in the river valleys around Kangole. In the dry season this ground is bare, parched and cracked like the land under the *Abutilon guineense-Triumphetta flavescens* community, mentioned above; but during the rains thousands of acres are covered with *Sorghum vulgare* growing up to 3 m. or more in height.

The *Sorghum* is grown in pure culture, but sometimes a little *Cucumis melo* L. is planted in admixture with it; small patches of *Arachis hypogea* L. (groundnut) are planted on more sandy patches of land. Besides the paths there is a tangle of annual grasses of which *Eriochloa nubica* Hack. & Stapf, *Setaria pallidifusca* Stapf & Hubb., and *S. verticillata* P. Beauv. are the most abundant. All the *Acacia seyal* trees are cut down on the farms, but occasional specimens of *Balanites aegyptiaca* Del. are retained for the value of their fruit, being merely pollarded; on uncultivated land there is usually a thicket of small trees of *Acacia seyal*, with an undergrowth of *Pavonia patens* Chiov.

The soil of the low ridges is said to be infertile and is not cultivated; it carries a sparse cover of low-growing annual herbs, notably *Tribulus terrestris* L., *Portulaca oleracea* L. and *Sporobolus arabicus* Boiss.; *Cyperus rotundus* L. var. *spadiceus* Boeck. is locally dominant in depressions on the ridges, where water lies at times during the rains. Near the settlements small plots of tobacco (*Nicotiana tabacum* L.) are planted, usually on old kraal sites; *Cucurbita maxima* Duchesne is grown in quantity; self-sown plants of potherbs are common, including *Gynandropsis gynandra* Briq., *Amaranthus spinosus* L. and *Chenopodium album* L.; their leaves are used extensively for food together with the leaves of other wild herbs such as *Tribulus terrestris* and *Corchoris olitorius* L.

Near the river banks there are many trees—*Acacia seyal*, *A. albida* Del., *Ficus* *gnaphalocarpa* A. Rich., *Tamarindus indica* L., *Kigelia aethiopica* Decne, *Balanites aegyptiaca*, *Ziziphus mauritiana* Lam. and *Z. mucronata* Willd. In most places the trees are scattered, forming an open woodland; but there are some patches of typical riverain forest, and there is little doubt that the forests would be much larger if the trees were not cut to provide poles and firewood and to clear land for cultivation; the species which are retained are mostly those with edible fruits; in the case of *Kigelia aethiopica* the fruits are not edible but are used in beer-making.

The largest areas of cultivation are around Kangole, especially to the east, there being many large fields between that settlement and Moroto; the same land is used year after year and, after the grain has been gathered, the stock are allowed to graze on the stalks, so that long before the end of the dry season the ground is quite bare. There is another large extent of cultivation around Kotido; the soil in this neighbourhood is more sandy than that of Kangole and well suited to groundnuts which are therefore an important crop. Nabilatuk, north of Kadam, is another centre of population with extensive fields; but cultivation is by no means confined to these large settlements for, wherever there are permanent water supplies and people are able to live permanently, they plant some crops during the rainy periods. Agriculture in Karamoja is subject to great risks because the rains often cease before the crops are mature and the plants are withered by the hot winds; the rain which does fall is in the form of violent storms, which are liable to wash away seeds or seedlings, and it is interesting that the Karamojong have a well-established system of piling weeds in lines along the contours of sloping plots in order to reduce erosion.

(5) *Grasslands in the east*

Away from the waterholes and rivers of eastern Karamoja there are tracts of grassland which are used for grazing in the wet seasons only, as their water supplies dry up soon after the rains cease. The most extensive of these grasslands lies between Moroto and Loyoro and is a level, almost treeless, tract out of which rise sharp isolated hills; Koten, claimed to be the original home of the Karamojong, is the largest of them. Although the grasslands are utilized only in the wet weather, they are grazed hard at that time and are never more than about 1 m. in height; and, by the time that they are left on account of shortage of water there remain only hard short stems, woody like bamboos, about 20 cm. high. Two grass species are codominant on wide stretches—*Pennisetum ramosum* and *Chrysopogon aucheri* Stapf; a small shrubby species of *Indigofera* (cf. *I. masukuensis*) is common in this grassland, and its persistence appears to be due to the fact that it is distasteful to cattle. Much of this grassland is open and free from trees, but on some of the lower, wetter places, the small stunted trees of *Acacia drepanolobium* are common; in these wetter spots *Setaria incrassata* is abundant.

The Karamojong cattle have become adapted to short supplies of water and can manage quite well if they obtain a drink only once in 2 days; this enables them to graze to a distance of 10 miles from the waterholes, moving out one day and returning the next. Therefore, up to this distance from permanent water, the grass is subject to grazing throughout the whole year and its composition is altered; the tufts of *Pennisetum* and *Chrysopogon* become sparser, until they disappear altogether. *Cynodon plectostachyum* is common in patches. But in most places no perennial grasses are to be seen and a great deal of bare ground is exposed for most of the year, there being a slight cover of ephemeral grasses during the rains—*Panicum atrosanguineum* Hochst., *Digitaria velutina* Beauv., *Dactyloctenium aegyptium* Richti., *Aristida adscensionis* L. and *Eragrostis* spp. *Barleria eranthemoides* R. Br., in the form of small rounded subshrubs about 30 cm. high, is characteristic of these grazed tracts, for it is so spiny as to be quite resistant to grazing (Pl. 5, phot. 6). Nearer to the waterholes the grasses become more and more sparse until none are left except for a few ephemeral species which appear during the rains; but the woody elements increase greatly, to such an extent that the aspect of the vegetation changes to that of a thicket, described below.

The eastern grasslands are all on lowlying dark-coloured clay soils; on higher land, both on top of low ridges and around the base of the hills, there are more woody elements, described below under the headings of woodlands and thickets. Beside the courses of the rivers also there is a dense growth of trees described under the heading 'Riverain forests'.

(6) *Riverain forests*

When the landscape of eastern Karamoja is viewed from one of the mountains during the dry season, the dark strips of forests along the courses of the rivers stand out in contrast to the parched grassland, and even in the wet season the trees are much darker in colour than the grass. These forests are evergreen; on the mountains they merge into the evergreen forests in the valleys; as the rivers proceed out into the plains, so the riverain forests become narrower and sparser, until they fade out in the swampy grasslands described above (Pl. 6, phot. 7).

Acacia albida is the dominant species in many stretches of this forest; it grows into magnificent specimens up to 20 m. in height, overtopping all other trees; the smaller *A. tortilis* Christensen is often associated with it and *A. seyal* is common, being dominant in places where the rivers fade into the swampy grasslands. *Terminalia brownii* Fresen. is another very common species of the riverain forests; *Syzygium guineense* DC. is locally common; *Kigelia aethiopica* is frequent; *Balanites aegyptiaca* is abundant in some of the lower places and *Tamarindus indica* is frequent on rather higher ground. Smaller trees of denser habit make a thick mass of foliage so that little can grow beneath them—trees such as *Ziziphus mauritiana*, *Craibia laurentii* De Willd. and *Carissa edulis*. A shrubby *Acalypha* sp. (cf. *A. frutescens* Forsk.) is locally dominant as undergrowth in some of the riverain forests. Even where there is dense shade, some undergrowth is found, especially the broad-leaved *Sansevieria dawei* Stapf and the spreading subshrubby *Crossandra nilotica* Oliv.; in more open places, the scrambling *Commicarpus plumbagineus* Standley is very common.

(7) *Woodlands in the east and north*

Most of the higher ground in the north of Karamoja is covered with forest of varying density—on the higher, hilly land the trees are relatively close, but on lower, flatter ground the trees are more widely spaced; in places they are so sparse that the formation would be better described as 'Grassland with scattered trees'. Most of the tree species in these woodlands are about 6–10 m. in height, and most of them are deciduous. There is a cover of grasses on the ground; in areas which are ungrazed, these grasses are up to 1½ m. in height, but in areas which are grazed the grasses are much shorter.

As in the higher woodlands around the mountains in the south of the district, *Combretum gueinzii* is abundant in many places; *Acacia* spp., especially *A. etbaica* Schweinf. and *A. holstii* Taub., are very common; *Cassia singuena* Del. is locally common; and many of the other species—*Bauhinia thonningii*, *Lonchocarpus laxiflorus*, *Gymnosporia sene-*

galensis, *Strychnos innocua*, and *Terminalia* spp.—which occur in the woodlands in the south, are also to be found in the north.

The grass species in these woodlands also are the same as those of the southern woodlands: *Themeda triandra, Setaria sphacelata, Chloris gayana, Panicum maximum, Eragrostis superba, Hyparrhenia* spp. and *Sporobolus pyramidalis* are all common species. The height and density of the grasses varies greatly according to the intensity of the grazing; there are no permanent water supplies on top of the escarpment north of Morongole and the grazing therefore is confined to the wet season, so that the grass is about a metre high. The valleys of the River Kidepo and its tributaries to the west and north-west of the mountain have been invaded by tsetse fly (*Glossina morsitans*), and cattle cannot graze there or they would soon die of trypanosomiasis; in these valleys the grass is 1½–2 m. high. South of Morongole there are stretches into which the fly has spread within the last few years; it is obvious that much of this land was heavily grazed in the past, but now there is a dense cover of *Themeda triandra*, a metre high (Pl. 7, phot. 9). Farther south, where the fly has not yet penetrated, grazing is still intense and has produced the usual effects—much bare ground with scattered plants of *Cynodon plectostachyum* and unpalatable weeds such as *Solanum incanum* Linn. and the spiny *Asparagus africanus* Lam.

The banks of the rivers carry a denser growth of trees resembling the riverain forest of the south: *Acacia albida*, *Terminalia brownii* and *Ficus gnaphalocarpa* are some of the most abundant species. Clearings for cultivations are made near the rivers for grain crops such as finger millet (*Eleusine coracana* Gaertn.), bullrush millet (*Pennisetum typhoides* Stapf & Hubb.), *Sorghum* and maize (*Zea mays* L.) which are grown in quantity when there is sufficient rain; scattered grindstones in areas which have not been cultivated for many years show that much more extensive cultivation formerly took place. There seems no reason to doubt the local tradition that the Dopeth, a grain-eating people now settled in the south of the Anglo-Egyptian Sudan, inhabited this area until about 40 or 50 years ago. When cultivations are made, the smaller trees are cut down, leaving only the larger specimens, with the result that, as in the south of the district, the character of the vegetation has been altered from that of a woodland to that of a grassland with scattered trees.

A densely wooded area of about 100 sq. miles, lying on the edges of the escarpment to the south-east of Morongole and known as the Timu Forest, represents the most well-developed woodland in north Karamoja. When viewed from a distance, this area appears to be a forest, with a continuous cover of trees; but on closer inspection it is seen to have a dense growth of trees near the rivers and on top of some of the hills, but that most of the land in the valleys and on the lower slopes of the hills is of open glades. *Ficus gnaphalocarpa*, *Albizzia coriaria* Welw. and *Acacia* spp. are the most abundant species of the riverain forests; in some parts *Euphorbia calycina* N. E. Br. is dominant: in the deeper valleys, the occurrence of *Phoenix reclinata* Jacq. and of *Croton macrostachys* Hochst. is indicative of fairly moist conditions.

The open glades of the Timu Forest also contain many specimens of *Euphorbia calycina*, together with *Combretum gueinzii* and many acacias, notably *Acacia holstii* and *A. hebacladoides* Harms. As in other parts of Karamoja, the grass cover in these glades varies in height and composition to the intensity of the grazing to which it has been subjected; for the Timu Forest is the main well-watered area of north Karamoja which has not yet been invaded by tsetse fly, and it is a very important grazing ground and carries a large concentration of stock, especially in the dry seasons. The parts which are some miles distant from the waterholes are covered with grasses up to over 1 m. high, in which *Hyparrhenia dissoluta*, *H. filipendula* and *Themeda triandra* are the most common species; but nearer the waterholes, the grass is shorter and sparser, and species indicative of heavy grazing, such as *Sporobolus pyramidalis*, *Chloris gayana* Kunth. and *Cynodon plectostachyum*, are more abundant (Pl. 7, phot. 10).

The tops of the hills, especially those to the north-east of the forest, are clothed with woodland of a type quite different to that beside the rivers. The dominant tree is *Olea chrysophylla* Lam. and with it is often associated *Dombeya quinqueseta* Exell.; when the *Dombeya* is in flower, the combination of its pink blossom and the grey leaves of the *Olea* gives an impression of cultivated peach trees and olives in the Mediterranean region, rather than of wild trees in tropical Africa. On some of the higher ridges, at an altitude of about 1800 m., there are small groups of *Juniperus procera* Hochst.; some of the older specimens are well-grown trees 30 m. in height, but there is little regeneration and few seedlings are to be seen.

Around the groups of trees on the ridges are tall grasses, typical of forest edges in the wetter parts of Uganda, belonging to species such as *Hyparrhenia cymbaria* Stapf and *Beckeropsis uniseta* K. Schum.; in the more open parts of the glades, *Themeda triandra* is abundant, growing to a height of 1 m. when it is not grazed too hard; but in many places the concentration of stock has caused the pasture to become more sparse with many tufts of *Sporobolus pyramidalis* appearing among the *Themeda*. The climate of the Timu Forest is much moister than that of most of the Karamoja district, a fact shown by the abundance of lichens and orchids epiphytic on the trees, and the forest forms an invaluable bastion against the advance of the semi-desert conditions of Turkana at the foot of the escarpment; but, if the ground cover is destroyed by over-grazing and the rate of run-off increased, the forest may soon die out.

Woodland covers the top of the escarpment and, in spite of the fact that it is exposed to the full blast of the hot dry winds from the east and is growing on thin stony soil, the vegetation is not of a markedly xerophytic type: *Combretum gueinzii*, *Acacia holstii*, *Terminalia brownii*, *Steganotaenia araliacea* Hochst. and *Boscia salicifolia* Oliv. are some of the more common tree species; *Cymbopogon afronardus* Stapf is the dominant grass at the summit of the slope. The escarpment falls steeply to an altitude below 1000 m. and conditions at the base are much drier than at the top; there are few trees, but frequent shrubs, among them an interesting xerophytic species of *Dracaena* (Th. 3254) not seen elsewhere in Uganda; *Loudetia flavida* C. E. H. is the dominant grass, growing in the spaces between the rocks.

(8) *Acacia woodlands and thickets in the east*

The grasslands and woodlands described above are to be found in the less accessible parts of eastern Karamoja, in places where water supplies are short or where the concentration of tsetse fly inhibits grazing of cattle; around most of the centres of settlement such communities have been replaced or are being replaced by *Acacia* woodlands and thickets. The thickets are of two types—deciduous and succulent—but they grade into each other and into the woodlands and grasslands. The most extensive development of *Acacia* woodland is around the base of Moroto, where this woodland replaces the *Combretum* woodland lying around the base of the other mountains and, together with thickets, it covers a wide belt of land stretching southwards from Moroto and eastwards from Kadam to the south-east corner of the district.

Acacia seyal and *Euphorbia calycina* are the two most common trees in much of the *Acacia* woodland near Moroto; other species of *Acacia*, notably *A. tortilis*, also are common (Pl. 8, phot. 11). Other tree species which occur in the *Acacia* woodland are more abundant in the deciduous woodland formations and may be regarded as relicts, notably *Tamarindus indica*, *Cassia singuenea*, *Terminalia brownii* and *Combretum gueinzii*. Smaller trees and shrubs include *Dichrostachys glomerata* Chiov., *Acacia pennata* Willd. (which forms large bushes up to 4 m. high and is locally dominant on many slopes), *Carissa edulis* Vahl and many others. Sparse tufts of perennial grasses—*Cenchrus ciliaris* L., *Heteropogon contortus* Beauv. and *Eragrostis superba* Wawr. & Peyr.—occur in some of the more open spaces, and the spreading *Cynodon dactylon* Pers., together with the larger *C. plectostachyum* Pilg., are common near paths. Much of the ground is bare for most of the year, and only in the rainy seasons does it carry a quantity of small tufted ephemeral grasses such as *Aristida adscensionis* L., *Tragus berteronianus* Schult. and *Leptocarydion vulpiastrum* Stapf.

The deciduous thicket is characterized by the dominance of deciduous trees and shrubs, many of them spiny, with an abundance of succulent plants in the undergrowth and a very sparse ground cover of grasses or other herbs. It varies in height according to the situation: around the base of Moroto it grades into the *Acacia* woodland, but out on the plains, where only shrubby plants abound, there are wide stretches only 3 m. high.

The lower thickets away from the hills are very variable in composition and in density—in some places the shrubs are so close that it is difficult to pass through them, while in others there are wide stretches of bare ground—but they have several features in common. Almost without exception, the thickets are on ground which is not flooded for any considerable time, for most of the species are intolerant of waterlogged soils. Species of *Acacia* are important constituents of the thickets, especially *A. mellifera* Benth., which is locally dominant on some of the flatter land, *A. orfota* Schweinf., *A. hebecladoides* Harms., *A. senegal* Willd. and *A. pennata*, which is dominant over large stretches of hilly ground (Pl. 8, phot. 12). *Albizzia anthelmintica* Brongn., *Balanites orbicularis* Sprague, *Terminalia spinosa* Engl. and *Cordia* sp. aff. *C. ovalis* R. Br. are species of small trees which are common in many parts of the thickets; in other places there are large patches where the spineless grey-barked *Lannea humilis* Engl. and *L. triphylla* Engl. grow to a height of 3 or 4 m. and often in pure stand, although *Commiphora* spp. are sometimes associated with them (Pl. 9, phot. 13). The *Acacia* thickets and the *Lannea* thickets grow in similar situations, sometimes close together and yet not merging, and it is difficult to understand the factors controlling their distribution; it is possible that the *Lannea* community is confined to the sites of former homesteads ('manyattas') or of former cultivations. Near the old kraal sites and by the waterholes groups of *Dichrostachys glomerata* and *Ormocarpum trichocarpum* Harms. are very common: in the puddled mud of the waterholes *Echinochloa haploclada* Stapf and *Panicum repens* L. are common.

Several species of *Grewia* are abundant in the thickets—*G. betulifolia* A. Juss., *G. mollis* Juss., *G. nyanzae* Drummond—and many Capparidaceae such as *Capparis rothii* Oliv., *C. tomentosa* Lam. and *Maerua* spp., which form scandent bushes. *Ipomea spathulata* Hall f. is very common; in the open it has a bushy habit, but when growing among taller plants it climbs to a considerable height. A striking feature of this thicket vegetation is the abundance of parasitic *Loranthus* spp. and *Viscum* spp. on many of the trees—

Loranthus curvifolius Benth., *L. dregei* Echl. & Zey., *L. dschallensis* Engl. and *Viscum bagshawei* Rendle, all growing on *Acacia* spp. and other species of *Loranthus* and *Viscum* on trees of other genera.

The trees and shrubs of the thickets are mostly deciduous, and for long periods are a mass of bare branches; the ground beneath is bare also in large stretches; and for most of the year the dark brown or grey bark of the trees and shrubs and the red-brown loam or yellow-brown sand of the soil is relieved only by the greenness of the succulent shrubs which are characteristic of this formation. The most common of the shrubs is *Sansevieria ehrenbergii* Schw. whose erect fan-shaped clumps of leaves are densely massed in many areas; the smaller procumbent *S. suffruticosa* N. E. Br. is more local in its occurrence. *Aloe* spp. are very common; there are at least four species in Karamoja, differing in size from massive shrubs with leaves a metre long to a small spreading species with leaves closely pressed to the ground. The *Sansevieria* spp. and the *Aloe* spp. often are growing on mounds slightly raised above the level of the bare compacted soil of the thickets; these mounds probably are due to the facts that the ground under the plants is protected from erosion and that the roots and stems tend to hold up the dust swept along by the wind near ground-level. *Sarcostemma viminale* R. Br. and *Cissus quadrangularis* L., both of which have climbing succulent stems, are very common.

The succulent thicket is confined to small areas, usually close to centres of settlement, and in these areas larger succulent shrubs are the dominant plants. *Euphorbia calycina* is locally dominant; other large *Euphorbia* spp., notably *E. breviarticulata* Pax. and *Euphorbia* sp. aff. *E. thi* Schweinf. are locally abundant. *Adenium honghel* DC., having a swollen stem and vivid pink or red flowers, is one of the most ornamental plants in the district; but it is very difficult to transplant, for even specimens which have small stems above ground have long thick fleshy tap roots of a surprising size (Pl. 9, phot. 14). *Kleinia longiflorus* Oliv. & Hiern. is frequent in the succulent thickets and, less commonly, in the deciduous thickets, for the two communities grade one into the other.

Succulent Stapeliads are much more common in Karamoja than in any other part of Uganda. There is a large *Caralluma* sp. which is up to half a metre in height; the smaller *Stapelia dummerii* N. E. Br. is very common, growing in the shade of groups of bushes; *Caralluma gracilipes* K. Schum. is local in occurrence.

A few species of perennial herbs are very common in the thickets, both in the deciduous thickets and in the succulent thickets; *Pentanisia ouranogyne* S. Moore with its blue flowers is very noticeable, for flowers of that colour are uncommon in tropical Africa; the succulent *Talinum cuneifolium* Willd. is abundant; *Dolichos oliveri* Schweinf. is locally common. While the rains are falling, and in places where there is little stock, ephemeral grasses appear during the rains, notably *Digitaria velutina*, *Sporobolus festivus* Hochst., *Tragus berteronianus* Schult. and *Microchloa kunthii* Desv. *Oxygonum atriplicifolium* Mart. and *Portulaca foliosa* Ker. are two very common quick-growing herbs. In areas where much stock is kept, the animals are so hungry by the end of the dry season that few of these annual species are allowed to grow, and the ground is almost as bare during the rains as during the dry season. Small shrubby spiny species of Acanthaceae, of which *Barleria eranthemoides* is the most common, and which are unpalatable to stock, form a large proportion of the ground cover in places where there is heavy grazing.

Most of the thickets are to be found growing on well-drained ground: as mentioned above, *Acacia seyal* and *A. drepanolobium* are the two species that form thickets on soil which is waterlogged for any considerable time, and associated with them is the grass *Pennisetum mezianum* Leeke. The soils of the thicket areas are compact loams, varying in colour from red-brown to dark brown; in many places the surface is covered with a layer of coarse sand or gravel which to superficial examination conveys a false impression of the true nature of the soil, for the covering consists merely of the residual coarser fractions of the soil which remain when the finer fractions are blown or washed away. Sheet erosion and gully erosion are very marked in the areas under thicket, especially near Moroto and Loyoro. Whether there is a covering of coarser fragments or not, the top layer of the loam is always very hard, even during wet weather and, as explained below, there is little doubt that it is the physical nature of the soil which largely determines the nature of the vegetation growing on it.

(9) *Mountain vegetation*

The woodlands which cover the lower slopes of all the mountains in Karamoja, with the exception of Moroto, the largest, have been described above. These woodlands extend to an altitude of about 2000 m.; *Combretum Gueinzii* is the dominant tree in these woodlands, while *Hyparrhenia dissoluta*, *H. filipendula*, *Themeda triandra*, *Brachiaria brizantha* and *Setaria sphacelata* are the most common grasses (Pl. 7, phot. 9). Near the base of the mountains there are outcrops of crystalline rocks and patches of poor stony soil; on these slopes *Heteropogon contortus* is the dominant grass. Higher up on Kadam and Napak, at an altitude of about 2000 m., on the steep cliffs of volcanic rock, *Crinipes longifolia* C. E. H. is locally dominant in large pendulous tufts; the occurrence of this grass is interesting, for it has been reported previously only from Mount Elgon, about 40 miles south of Kadam.

Most of the slopes of Kadam at altitudes between about 2000 m. and about 2500 m. is clothed with evergreen forest; the cliffs are almost bare and there are numerous rocky knolls on which *Cymbopogon validus* Stapf and *Sporobolus* sp. is dominant. But the rest of the ground is under a dense cover of trees (Pl. 10, phot. 15); *Podocarpus milanjianus* Rendle is one of the tallest species, attaining a height up to 30 m.; *Chrysophyllum* spp. are abundant; *Antiaris toxicaria* Lesch., *Teclea nobilis* Del., *Syzygium guineense* DC., *Croton macrostachys* and *Conopharyngis holstii* Stapf are common trees. *Dracaena fragrans* Ker Gawl, *Lobelia gibberoa* Hemsl. and *Senecio multicorymbosus* S. Moore, are some of the more common shrubs; the forest grass, *Setaria caudula* Stapf, is common. At an altitude of about 2000 m., as on many other Uganda mountains, there is an abundance of epiphytic orchids, and it seems that the atmospheric humidity at this elevation is especially high.

Precipitous cliffs surround the plateau at the summit of Kadam, at an altitude of about 3200 m.; the plateau is covered with mountain moorland of two types—grass moorland and shrubby moorland. The grass moorland consists of tussocks of grasses growing to ½ or 1 m. in height and is restricted to patches of shallow soil over the rocks (Pl. 11, phot. 17). *Exotheca abyssinica* Anderss., *Eragrostis lasiantha* Stapf, and *Tripogon liebenbergii* C. E. Hubb. are the most common species, and *Setaria sphacelata* Stapf & Hubb. is locally dominant in crevices of the rocks; the small shrubby *Heliohrysum fruticosum* Vatke is very common; in swampy places the prostrate *Alchemilla kivuensis* Engler is locally dominant.

The shrubby moorland which covers the deeper soils on the summit of Kadam consists of a dense growth of *Protea abyssinica* Willd. about 1½ m. high, in many places admixed with *Erica arborea* L. (Pl. 11, phot. 18); beneath the bushes the grass *Eragrostis volkensii*

Pilger. is dominant, scrambling up the bushes. At the upper edge of the forest there are other common woody species—*Faurea arborea* Engl., *Berberis holstii* Engl., *Myrsine africana* L., *Cluytia richardiana* Muell Arg., and *Anthospermum pachyrrizum* Hiern.; some of these grow to a height of 3 m.

The majority of the small trees and shrubs in the shrubby moorland have small thick leaves (for the broad-leaved arborescent *Senecio* spp., which are abundant in valleys and swamps on the higher mountains of Uganda, do not occur in Karamoja) and are markedly xerophilous in comparison with the woody elements in the evergreen forest below; it seems that less rain falls on the summits than on the forest zone, and that the rate of evaporation may be higher. The name 'Tropical alpine elfin-woodland' postulated by Burtt Davy for this formation, is an unhappy one, for in this zone it is the shrubs, rather than the trees, which are the dominant elements, and the growth of most species is upright, rather than oblique. The nomenclature appears to be founded on Volkens's description of Kilimanjaro vegetation, which does not convey a very true picture of the plant formations on that mountain where the areas of grassland above the forest zone seem to be largely due to the effect of fire; the development of *Usnea* on the branches is more abundant in the forest zone at about 2600 m. than above that altitude; and the growth of the shrubs becomes more stunted and compact as the altitude increases until the moorland merges into a desert at an altitude of 4500 m. The term 'moorland', besides being descriptive of the life form of the higher zones of vegetation on African mountains, also conveys a feeling of the dull colouring so characteristic of this vegetation: the brownish tufts of grass and the dull green or grey foliage of the shrubs produce an effect quite different from the vivid green and bright masses of flower on an alpine meadow. It is much more difficult to climb up to the plateau of Kadam than to the moorland areas of other East African mountains, a fact which may explain the preponderance of shrubby moorland on this mountain and the absence of the large stretches of grassy moorland seen on other mountains; for it is probable that the shrubs represent the true climax vegetation and the invasion by grasses is due to the effects of fire.

Napak is much lower than Kadam, the summit being about 2500 m. above sea-level. The steep lower slopes are covered with low open deciduous woodland in which *Combretum gueinzii* is dominant (Pl. 10, phot. 16); above 2100 m. the trees become thicker and there are patches of closed forest in the ravines. *Albizzia zygia* Macbride, *Cordia abyssinica* R. Br., *Pittorosporum abyssinicum* Harms., *Olea chrysophylla*, *Croton macrostachys* and *Phoenix reclinata* Jacq. are common trees and *Dombeya leucoderma* K. Schum., *Cluytia abyssinica*, *Trichocladus malusanus* Baker and *Musa* sp. are common shrubs in these forests; *Hyparrhenia cymbaria*, growing to a height of 2 m., is dominant in some open glades. At the upper edge of the forests, *Acacia stenocarpa* Hochst. and *Dombeya quinquiseta* Exell. are common trees. The rocky summit is covered with grass moorland in which *Exotheca abyssinica* is dominant and *Setaria sphacelata* and *Digitaria scalarum* Chiov. are abundant; there are large stretches of *Pteridium aquilinum* Kuhn. A few families of Dopeth, the people who inhabited Karamoja before the advent of the Karamojong, still live on Napak; they eat wild plants such as *Dioscorea schimperiana* Hochst., they keep a number of cattle and do a little cultivating, but seem not to endanger the cover of vegetation on the mountain.

Morongole in the north of the district exhibits the same zonation of vegetation—woodland, forest and moorland. *Combretum gueinzii* and *Acacia etbaica* are the dominant trees in the woodland; *Themeda triandra* and *Setaria sphacelata* the dominant grasses. The closed forest above 1900 m. is composed of *Teclea nobilis*, sometimes in pure stand, sometimes mixed with large specimens of *Ficus* spp.; above 2200 m. the dominant tree in the forests is *Dombeya elliottiana* K. Schum. and *Cussonia spicata* Thunb. is common; there must be a fairly constant high humidity at this altitude, as there is an abundance of the grey pendulous lichen *Usnea longissima* Ach. on the branches. The upper edge of the forest, at about 2400 m., grades into shrubby moorland of a thick mass of shrubs and small trees—*Protea abyssinica*, *Faurea speciosa*, *Hypericum lanceolatum*, *Anthospermum usambarense* K. Schum., *Myrsine africana* and *Berberis holstii*—mixed with *Pteridium aquilinum*. The shrubby moorland in turn grades into grassy moorland which covers the summit of the mountain; *Exotheca abyssinica* is the dominant species in the grassy moorland; *Setaria sphacelata*, *Hebenstreicia dentata* L., and *Helichrysum fruticosum* are common.

The vegetation of Morongole exhibits interesting affinities with that of the nearest large mountain group—the Imatong Mountains, situated on the border between Uganda and the Anglo-Egyptian Sudan, 80 miles to the west. In the grassy moorland at the summit there grows the shrubby *Coleus grandicalyx* E. A. Bruce, very decorative on account of its vivid blue flowers and purple bracts, which previously has been reported only from the Imatongs. Many of the herbaceous species are the same as those on the Imatongs; for example, *Setaria splendida* Stapf has been found on both mountains, but nowhere else in Uganda. There is also considerable resemblance between the ravine forests of the two mountains; in these forests *Dombeya elliottiana* is locally dominant and a tall succulent *Euphorbia* sp., not seen elsewhere in Uganda, is frequent. In other respects the vegetation of Morongole resembles that of the other Karamoja mountains; in the grassy moorland on the summit, *Tripogon liebenbergii* is common, as on all the others; this species has not been reported outside the Karamoja district.

Just as the vegetation around the base of Moroto differs from that around the other mountains of the district, so also does the vegetation on the slopes of the mountain. Patches of closed forest occur in the ravines; *Ficus* spp., *Erythrina abyssinica* Lam., *Croton macrostachys*, *Maesa lanceolata* Forsk. and *Carissa edulis* are some of the more common species. Many cattle were kept on the mountain, with the result that all the ground cover has been heavily grazed; while the canopy overhead has prevented the rain from beating in full force on the soil, yet there has been little undergrowth or litter to prevent the water from rapidly running off the steep, rocky slopes.

Above 2400 m. the forest grades into woodland of scattered, rather stunted, shrubs and small trees such as *Faurea arborea* Engl., *Protea abyssinica* and *Lachnophylis congesta* C. A. Smith, all less than 4 m. in height; there are occasional stunted specimens of *Juniperus procera* (Pl. 6, phot. 7). The woody elements become sparser with increasing altitude, until at the peaks the vegetation becomes grassy moorland similar to that on the other mountains. A few of the species collected on Moroto seem to occur nowhere else in Karamoja; one interesting record is that of *Campanula rigidipila* Hochst. & Steud., the only member of the genus known to grow in Uganda. Although the majority of species are common to other mountains, yet the general aspect of the western slopes of Moroto is quite different from the others. Instead of the well-defined zones of forest, shrubby moorland and grassy moorland, there are large stretches of stunted woodland, which in some places is almost thick enough to be classed as a thicket. And there is no doubt that, just as grazing has transformed the woodland at the base of the mountain to a thicket, so also grazing and burning have completely altered the mountain moorland; for, on the eastern slopes, where these influences have been less marked, the vegetation is more like that of the other mountains. It is unlikely that the differences can be attributed to meteorological factors; for Moroto is nearly as high as Kadam and is nearly as large in area; it is much higher and more extensive than Napak or Morongole; therefore it is probable that it receives a rainfall as heavy as that of any other mountain in the district.

DISCUSSION

The vegetation of Karamoja shows an interesting pattern—out on the plains, where the average annual rainfall does not appear to be more than about 25 cm., there are large areas of grassland; around the smaller mountains, where the rainfall is a little higher, there are belts of woodland; but near the rivers in the east of the district, where the rainfall is higher still and in situations which are sheltered from the dry east winds, a more xerophilous vegetation of acacia woodland or deciduous thicket is growing. The more markedly xerophytic plant community, the succulent thicket, is found only near centres of dense population of man and stock, in localities where there are good supplies of water.

The Karamojong are a pastoral people, dependent on their stock for food, and they would naturally tend to settle in places where there is an abundance of water and grazing. The main concentration of the tribe has been near the rivers to the west of Moroto; settlement near the other mountains was not so dense, as such outlying areas were frequently raided by other tribes. The average annual rainfall at Moroto is 90 cm. and is fairly well distributed; many rivers arise on this mountain; yet it is in this neighbourhood that there is the most striking development of semi-desert vegetation for, in place of the broad-leaved woodland around the other mountains, there is acacia woodland and thicket.

It seems that the present aspect of the vegetation in the east of Karamoja has been determined not only by the rainfall and the soil, but also by the effects of settlement, cultivation and grazing; this view is supported by the weight of native tradition, which asserts that formerly the grass was more abundant and vigorous. At the present time near Loyoro there is little grass that is as much as 1 m. in height—occasional tufts growing in *Sorghum* fields are carefully preserved for thatching; yet it is affirmed that within living memory, about 30 or 40 years ago, dense grass up to 2 m. in height covered the countryside which now is under thicket.

Further proof that the thicket growth is due to the effects of prolonged and continuous grazing is to be seen in the contrast between the areas near the waterholes in the west, which are grazed very short in the dry seasons only, and those in the east, which are grazed throughout the whole year. Although the herbage on the western grazing grounds is much shorter than that at a distance from the waterholes, yet it forms a good cover; but the ground near the settlements in the east is almost bare except for scattered woody plants, succulents and spiny subshrubs. Where there is a permanent population of stock, any palatable herbs are grazed back constantly until they are killed. Every year the soil of the western grazing grounds may be nearly bare by the time that they are vacated at the end of the dry season, yet the grasses are able to recover during the rains and a good cover of herbage is maintained. There is an increasing volume of evidence from pasture research in temperate and subtropical regions that it is essential for rotational grazing to be practised if the quality of a grassland is to be maintained, for, unless the herbage is allowed to grow unchecked during part of the year, the more palatable and nutritious species will be killed out. It is not surprising therefore that a long period of continuous and intense grazing has resulted in the ruination of the pasture in the east of Karamoja.

More evidence that over-grazing is responsible for the condition of the land and the vegetation is afforded by the recovery of the grasslands in the north of the district after they have been invaded by tsetse fly. Areas around Kakumari, which showed abundant evidences of overgrazing—the gullies, the patches of scrub, the old kraal sites covered with *Cynodon* grass—within 3 years had recovered to a remarkable extent and were covered with grasses a metre high; *Themeda triandra* was dominant on the higher ground and *Setaria incrassata* in the hollows; fires had swept through these areas and had killed off many of the smaller trees and shrubs. The valley of the River Kidepo, near the Sudan border, which was invaded by tsetse many years ago, represents a more advanced stage of this recovery, for the grass there is 2 m. high and the trees are sparser.

Small plots at Loyoro, protected from grazing by hedges of thorn branches, have shown how much recovery is possible in less than one year. These plots were enclosed on a hillside of compact red-brown soil, typical of the land under thicket, and bare except for a few scattered shrubs. At the end of 6 months, during which only sparse rains fell, these plots contrasted strongly with the land around, which was as bare as when the plots were enclosed. One plot, on hard unbroken soil, was covered with ephemeral grasses and herbs—*Sporobolus festivus*, *Eragrostis* spp., *Aristida* spp., *Dactyloctenium aegyptium*, *Hackelochloa granularis*, *Oxygonum atriplicifolium* and the perennial *Solanum incanum.* A second plot, laid down across a gully, showed even more interesting results, for, in addition to the ephemeral plants, perennial grasses were growing strongly in the gully and spreading out from it; the species were *Cynodon plectostachyum*, *Cenchrus ciliaris* and *Panicum hanningtonii*. A third plot, enclosed on farm land, included one of the contour rows of weeds, and it was from this bund that the most abundant growth of perennial plants—*Barleria eranthemoides*, *Cynodon plectostachyum* and *Commelina kotschyi*—was commencing to spread: recovery on this third plot, which had been cultivated, was more rapid than on the other two enclosures.

There appear to have been two reasons why the herbs grew best on the cultivated ground—first, because the hard surface crust had been broken and, secondly, because there was no competition for soil moisture as with the roots of the shrubs growing on the uncleared ground. The *Acacia* trees and shrubs of the thickets have very extensive root systems, as shown by Gillett (1941) in the case of similar communities in Somaliland; it is difficult for seedlings to become established in competition with such roots under the sparse rainfall of Karamoja. This fact is well known to the Karamojong and is the reason why they undertake such arduous clearing for their cultivated land; all *Acacia* spp. are cut down or removed, but other species such as *Balanites mauritiana*, whose roots will not compete so vigorously with crops, are allowed to remain; hence former farmlands are sometimes characterized by pure stands of *Balanites*.

Much has been written about the effect of cultivation, grazing and burning in diminishing the growth of woody species in the tropics and subtropics, but the vegetation of Karamoja shows that some woody plants—those of the thickets—are encouraged by these processes. *Dicrostachys glomerata* is widely distributed in Uganda, being locally dominant in small patches; examination and inquiry almost always prove that these patches have been the sites of settlements. *Acacia holstii*, another widely distributed species, frequently indicates settlement or intensive grazing; for example, in the district of Ankole, where the rainfall is little more than that of Karamoja, and the vegetation is open grassland or sparse deciduous woodland, in the rainy season the pale green of the landscape is patterned with darker patches, usually in folds of the hills or on their lower slopes, where thickets of *A. holstii* denote the sites of former camps.

It seems probable that the woodlands and thickets of *A. seyal* and *A. drepanolobium*, so marked a feature of the vegetation on the lower ground in eastern Karamoja, may also be due to the effects of grazing and trampling; the spread of these *Acacia* spp. may be encouraged by stock which browse on their pods. Thickets of these species are to be found in abundance beside rivers and hollows where the grazing has been intense; they are sparse in the south-west of the district, where similar hollows on similar soils are to be found, but where there had been much less grazing. It is interesting to note that *A. drepanolobium* grows as a stunted small tree or large bush on the seasonal swamps of Karamoja, seldom having a height of more than 4 m. or a spread of more than 3 m.; yet the same species forms a medium-sized tree with the typical flat-topped *Acacia* habit when growing on the well-drained slopes of volcanic ash at an altitude of about 2300 m. on the slopes of Longonot, an extinct volcano in Kenya. The habitats appear to be very different in regard to water supply and texture of soil; the fact that the *Acacia* is relatively stunted in Karamoja may indicate that it is of secondary growth there.

A. pennata, which forms so important a constituent of the thickets of hilly ground in eastern Karamoja, grows in many parts of Uganda. It is by no means to be regarded as a xerophytic species, for it grows commonly as a liane in secondary forest in regions of high rainfall; it is also common in drier areas, where the typical vegetation is deciduous woodland, growing in cracks of exposed rocky masses on the tops of hills; and it is locally dominant in the thickets of eastern Karamoja. These habitats cover a wide range of soils and climates, but they have one feature in common—they are not exposed to fire. The dry stems of *A. pennata* are very inflammable, and there seems no doubt that immunity from fire is one of the major factors controlling the distribution of the species.

The majority of the woody plants in the thickets are low-growing shrubs or small trees, with a thin bark on their stems and branches; in these respects they are in contrast to the species typical of deciduous woodland, whose bark is thick and corky and whose leaves and twigs form a canopy at a height of about 4 m., somewhat above the full effect of a fire in the grass near ground-level. While all the ground cover is grazed away, the thickets are immune from fire; but, as mentioned above, when the grass is allowed to grow sufficiently to provide material for burning, the number of the shrubs may be rapidly reduced, for the small ones are killed by fire. As soon as the grasses are free from the competition of the roots of many woody species, they can grow with increasing vigour and the area may revert to grassland or to deciduous woodland.

This type of woodland, so well represented in Uganda as in other East African territories, is most valuable both from the aspect of soil preservation and for the provision of good grazing. The presence of the trees appears to improve the quality of the grassland, although there is evidence that, on account of root competition, the bulk of herbage may be reduced. Some of the more palatable grasses—and the same species appear to be the most nutritious—are more abundant under trees than in the open. Shade may be a factor in determining this distribution, but it seems that soil factors are more important, for the most nutritious grasses will grow only on the better soils. The trees have a most important siphon effect—by means of their deep root system they bring up mineral plant nutrients from lower layers and deposit them on the surface of the soil. There is, as yet, little direct evidence in proof of this phenomenon, but there is much indirect evidence in the rapid loss of fertility that ensues when the trees are cut out, giving rise to the grasslands, open or with scattered trees, sometimes termed 'Cultivation steppe'.

When the climate will support woodland, the retention of this community is desirable. But continuous grazing will soon lead to rapid deterioration of the herbage, to the loss of soil cover and erosion and the transformation of woodland to thicket; under the relatively sparse rainfall of Karamoja the alteration of the plant community will be very rapid. Even in wetter areas, however, overgrazing leads to rapid deterioration of the deciduous woodland: striking examples may be seen in the thickets, mostly of evergreen shrubs, with bare eroded ground beneath, which are so abundant near the edges of swamps in the Lake Kyoga basin.

THE INFLUENCE OF MAN AND STOCK ON THE SOILS

The soils of the Karamoja district show great differences in their physical and chemical characters. A number of samples have been tested for reaction with B.D.H. Universal Indicator and the available nutrients—nitrates, phosphates, potassium and calcium—have been estimated by Spurway's method (1938); the results are fairly consistent and there are definite correlations between the soil types and the plant communities growing upon them.

The valley grasslands are on clay soils, dark brown, dark grey or almost black in colour. Such soils are alkaline, having a *p*H value of about 8·0: they are fairly well supplied with phosphates and potassium and are very rich in calcium; nodules of calcium carbonate may be seen on the surface and in the upper layers of the soil. These dark calcareous clays are exceedingly sticky when wet; walking or wading across the valley grasslands in the rainy seasons is very tiring work; and it is impossible to camp in the valleys at these times because there is so little percolation that water stands in pools and puddles for long periods.

Most of the areas under deciduous woodland have red-brown loamy soils, less alkaline in reaction than the soils in the valleys and containing less calcium, but well supplied in phosphates and potassium; the reaction is usually slightly acid with a reaction of about *p*H 6·5 or *p*H 7·0. The woodland soils are better drained than those of the valley grasslands and water does not stand on them for long periods. These woodland soils appear to be derived from the same types of wind-borne and water-borne deposits as those of the grasslands in the valleys; Milne (1936) has shown how by virtue of fluctuations in climate (wet-season waterlogging and dry-season aridity) alluvium may be transformed into 'mbuga' soil, i.e. calcareous clay.

The areas under thicket and also the cultivated lands are usually dark brown, red-brown or almost black in colour: often the real nature of the soil is obscured by a superficial layer of sand or gravel, left when the finer particles were washed or blown away. These soils are usually neutral or alkaline in reaction and well supplied with phosphates, potassium and calcium; in fact, on the basis of available plant nutrients, they are some of the richest soils in Uganda. The soils of the thickets, with the exception of the *Acacia seyal* and *A. drepano-*

lobium thickets which grow on dark calcareous clays like those of the valley grasslands, have one very striking feature: the superficial layers are very hard, like cement.

The zonation of vegetation on the mountains may be correlated with the soil types. The soils of the forest zone usually are dark-coloured, rich in humus and in plant nutrients, and alkaline in reaction. The moorland soils, on the summits of the mountains, in contrast to all other soils in the district, are markedly acid, with values of about *p*H 4·5 or 5·0, and contain little or no calcium. These soils are dark in colour and peaty in texture, and there seems no doubt that their characters are due to the relatively low temperatures, which permit the accumulation of much organic matter.

It is not surprising that the soils, both of cultivated lands and of thickets near the centres of settlement, should be so well supplied with plant nutrients. Large numbers of stock disperse from these settlements to graze and return to sleep and to drink; they are bound to add to the store of nutrients in the soil near the settlements by their excrement. Although there is such an accumulation of nutrients, yet the sites of abandoned kraals remain bare for years and even then are colonized only by certain species; *Cynodon plectostachyum*, whose local name 'Kalandalugo' means 'by the cattle kraal', is one of the most prominent. On house sites the accumulation of ashes from fires completely alters the composition of the soil.

It seems that in some cases the accumulation of nutrients is so marked as to be toxic in action but, in addition to the chemical factors, physical factors also are involved. The trampling of man and stock produces such compaction of the soil that its physical structure is badly affected and, even when the hard crust is broken by cultivation, the effect persists for many years: some regularly spaced, stunted, circular patches in a field of millet at Loyoro were explained as the sites of the lines of the King's African Rifles in 1921—the lines had been occupied for less than 18 months, but the effect had persisted for more than 18 years.

House sites and kraal sites have covered only a small fraction of the land, but the trampling of the stock has affected the whole countryside for many miles around the settlements. The huge flocks and herds, walking, grazing and browsing, have had an enormous cumulative effect and there can be no other explanation of the compaction of the surface of the soil. Persistent grazing, in addition to treading, must have an important effect on the soil, for it inhibits the formation of a cover of annual weeds which, by the growth and death of their roots, would make the surface layers more permeable. So hard are these layers in the thicket areas that the rain cannot penetrate to any depth; this fact is strikingly demonstrated in the wet seasons when, although there are heavy rainstorms every afternoon, yet the ground remains so hard that it is very difficult to dig a shallow trench around a tent in order to protect it from being flooded. The upper centimetre or two may be moist, but the soil below is as dry and as hard in the rainy season as in times of drought.

The lack of percolation into the soil is the reason why, under a fairly well-distributed rainfall of 90 cm., the vegetation may be dominated by xerophytic species, such as might be expected under semi-desert conditions. So small a proportion of the rainfall is absorbed by the soil and becomes available to the plants that they are in fact living under semi-desert conditions; the figures of rainfall are of little significance in relation to plant life when most of the water runs off the surface. It is on account of the volume and rate of the run-off that sheet and gully erosion are so marked in the thicket areas; once the hard surface layer has been penetrated, the soft even-textured subsoil is rapidly eroded and deep narrow gullies are formed, as are typical in soils of loessial origin.

Some of the worst examples of this gully erosion are to be seen near Loyoro, where there is a large concentration of stock on hilly ground and where most of the uncultivated land is covered with thickets. There are a few low hills whose rounded tops are free from bushes and are covered with a dense short turf of *Cynodon plectostachyum*, which has persisted in spite of the heavy grazing. All the finer particles of soil have disappeared from these hill tops and the grass is growing on a coarse-grained subsoil of comminuted rock fragments; in spite of all the trampling, this ground remains permeable to rain water, a fact which appears to explain the persistence of the grass.

Apart from the physical effect of the lack of soil moisture in and beneath the compacted layers, there is the chemical effect of the accumulation of bases in the soils near the settlements, an effect intensified by the lack of percolation. Even in the wetter parts of Uganda, with an abundant rainfall and an abundant percolation, the concentration of bases will persist for a long period on the site of settlements; for example, when tea (a calciphobe) was planted in the west of Uganda on land which had been uninhabited for 40 years, the plants would not grow on certain spots which, from the abundance of potsherds, obviously were house sites.

Dicrostachys glomerata is a species widely distributed in both the wetter and the drier areas of Uganda, but which is seldom found except on old house sites or kraal sites. The concentration of bases in the soil appears to be the factor controlling the distribution of the plant, a hypothesis supported by the fact that in one locality it does grow away from house or kraal sites—at Sempaya in the Semliki valley, where *Dicrostachys glomerata* is locally dominant on the very alkaline soil around the hot springs and where, instead of being merely a bush or stunted small tree, it grows into large specimens up to 10 m. high and having a wide spread.

Many species in the succulent thickets seem to require soils rich in bases as well as dry conditions. *Euphorbia calycina*, the dominant in many of them, is a common tree in Uganda. It grows in some regions of heavy rainfall, often being rooted in cracks among the granite masses exposed on hill-tops; in other areas it is confined to anthills, where there is an accumulation of bases; and on the Lake George flats where, as in Karamoja, the soils are rich in lime, the tree grows widespread in the grassland. Drainage may be a factor involved in this distribution, but it does not appear to be of paramount importance, as some of the localities on the Lake George flats, where the *Euphorbia* is abundant, are very wet for part of the year. In Karamoja also the xerophytic appearance of *Euphorbia calycina* does not accord with the distribution of the species: it is absent from the wind-swept steep slopes of the escarpment, but is abundant in the sheltered valleys on the west of the mountains and in the valleys of the Timu Forest.

The other species of *Euphorbia* in Karamoja are more local in their distribution, being confined mostly to the deciduous thickets, on compact alkaline soils; there are two notable species which are exceptional to this statement, but which nevertheless are growing on soils rich in bases—the tall tree species in the ravine forests of Morongole and a smaller spreading tree on the slopes of Kadam, which also grows on Tororo Rock, the most notable example of limestone in Uganda.

The Stapeliaeae also appear to have a strong preference for soils well supplied with bases, such as occur near settlements in Karamoja. Living specimens of this family, planted on poor leached soil in the Botanic Gardens at Entebbe where there is a relatively high rainfall, grew poorly, dying off and rotting in patches. Their condition improved greatly after heavy dressings of wood ashes had been applied, and normal growth was resumed. One species, *Stapelia dummeri*, has proved to be more tolerant of the climate and soil conditions in the west of Uganda; in fact, this species was named from specimens cultivated in native gardens, and Karamoja is the only district in Uganda where the plant has been found in the wild state.

MEASURES TO IMPROVE THE CONDITION OF KARAMOJA

Karamoja district occupies an important place in acting as a barrier between the arid areas in the north of Kenya and the moist, fertile lands of the Teso district of Uganda; violent dust-storms, darkening the sky with a red-brown haze, sweeping over from Turkana, are a vivid reminder of what may happen to Karamoja if preventive measures are not put in hand. The effects of overgrazing are cumulative—the larger the areas which are ruined, the greater the concentration of stock on the remaining grasslands; the available pasturage may be further reduced by the spread of tsetse fly.

The present population of domestic animals in Karamoja is larger than the district can carry without further deterioration of the vegetation, and it will have to be reduced. With so uncertain a climate, the people cannot depend on agriculture alone; stock must constitute a vital part of the food supply, but the present numbers of cattle are larger than are needed to supply the wants of the people; some families have small herds, while others have a large excess; it is the large numbers of unutilized cattle which constitute so grave a menace to the vegetation. Therefore the Karamojong are being persuaded to dispose of some of the surplus cattle and the scheme is meeting with some success, although they are very loath to part with any animals. (It is hard for a European to understand the attachment of the pastoral African tribes to their cattle—it is not merely a question of wealth or ownership, but an almost religious bond, allied to the ancient Egyptian worship of Hathor, and probably derived from the same roots.)

Water supplies are being developed, both by boreholes and by surface catchment tanks, in order that all available grazing may be utilized to the fullest extent. This work is being combined with measures to prevent the spread of tsetse fly. The south-western part of the district has been declared a Crown Forest in which grazing will be permitted only during the dry seasons for, as pointed out above, hard grazing may be allowed at that time if the grasslands are allowed to make full growth during the rains. All the mountains of Karamoja, with the exception of Napak, are closed to settlement, grazing and honey gathering, for that industry is the cause of destructive fires in the forests.

When the whole of the grassland in Karamoja has been provided with water supplies and when the number of stock has been reduced, it will be possible to close some of the eastern areas for spells to allow them to regenerate. Regeneration would be hastened if the impervious surface crust of the soil could be broken by some form of contour ploughing; this would be an expensive operation to be carried out on a large scale, for powerful machinery would be needed and the rough terrain would lead to much wear and tear. A more feasible method would be to cut down the trees and shrubs to lessen the root competition with the grasses and herbs; this woody material, if laid on the ground, would soon be broken down by termites to form a cover to absorb water and to slow down the run-off.

If any cultivation or soil-breaking were undertaken, it might be combined with the planting of *Cynodon plectostachyum* and *Cenchrus ciliaris*, rapidly growing drought-resistant grasses, which are used for soil colonisation in Tanganyika (Staples, 1942). No other local grass would appear to be of much value for planting; many of the most useful tropical pasture and fodder grasses—ranging from *Pennisetum purpureum* Schum. (elephant grass) to *Pennisetum clandestinum* Hochst. (Kikuyu grass)—are to be found in large or small amounts in Karamoja, but in many instances they are local in occurrence, for only in restricted areas are conditions suitable to their growth; it would therefore be a waste of time to plant them on a large scale.

The semi-desert conditions in the district seem to be of recent origin; exotic grasses, imported from older desert areas, might be of value. The introduction of drought-resistant browse plants, such as *Prosopsis chilensis* Stuntz, would provide an immediate increase in stock food; but it is probable that the *Prosopsis* might become naturalized on a large scale, as in India, around Delhi, and might hinder the return to grassland. There seems little doubt that if there is a choice between browsing and pasturage, the latter is preferable because it provides a larger amount of food for stock and a much better cover to the soil to prevent erosion.

BIOLOGICAL FACTORS IN TROPICAL ECOLOGY

Karamoja is much drier than the rest of Uganda, and the only other district of the Protectorate which resembles it in vegetation is Chua, which lies to the north-west (Eggeling, 1938). In other East African territories, however, there are large areas of similar dry grasslands, woodlands and thickets (Phillips, 1930; Edwards, 1940; and Burtt, 1942). The vegetation communities described by Phillips and Burtt from Tanganyika are very similar to those of Karamoja and many of the species are identical.

There are considerable differences between the interpretation of plant successions given by Phillips and those which are outlined above. Phillips referred to the 'Deciduous scrub climax', which corresponds in appearance and composition with the thickets of eastern Karamoja; the facts that these communities are found only where there is intensive grazing and that they alter rapidly when the cattle are excluded on account of tsetse fly would seem to show that the Karamoja thickets must be regarded as 'Disclimaxes', defined as those communities that originate and are maintained by disturbance (Clements & Shelford, 1939). It seems that disturbances also must have been involved in Tanganyika, for Phillips showed successions of both the hydrosere and the xerosere through the 'Combretum—other species woodland' (termed in this paper 'Deciduous woodland') to 'the deciduous scrub climax'.

In the valleys to the west of Karamoja, where the effects of settlement and grazing have been least marked, there are large stretches of open grassland; it appears therefore that these grasslands may be regarded as climax communities and those areas near settlements in the east, where many specimens of *Acacia drepanolobium* and *A. seyal* are growing in the grasslands, may be considered as disclimaxes. This hypothesis also is contrary to Phillips, who stated: 'The grassland areas are seral, not climax.' In the same paper Phillips briefly discussed the effects of fire, a subject of great complexity, and most of the results listed by him are deleterious. In Karamoja, the fires which are started on the mountains by the honey collectors, who use smoke to overcome the wild bees, are responsible for great damage and have destroyed large areas of forest. The Karamojong also make special visits to the grasslands in the west in order to burn the grasslands before the end of the rainy season, so that there might be a flush of young grass for the dry-season grazing; from the appearance of the vegetation, it seems that such fires do not have a bad effect. Early burning does not seem to do great harm to many species which are common in the deciduous woodlands of East Africa; in fact, it seems that burning is essential if the seeds of some trees, for example *Butyrospermum parkii* Kotschy., are to germinate well. In addition, there must be an important indirect effect from the destruction of grasshoppers and other insects by fire; those which endeavour to escape are captured by the large flocks of birds which congregate at the edge of grass fires, gorging themselves so much that sometimes they are unable to fly.

Burtt (1942) has stressed the point that many of the shrubs in the thicket communities are easily killed by fire. The 'hard pan' soils that he described and the vegetation growing on them closely resemble the thickets and soils near settlements in Karamoja. He mentioned that the hard pan was not at the surface, as in Karamoja, but was situated at a depth of about a foot; similar hard pans, and sometimes two or three of them one above the other, may be seen exposed on the vertical sides of river courses in eastern Karamoja, where it is obvious that they are buried land surfaces. It therefore seems probable that the 'hard pans' in Tanganyika may have been formed by the trampling of wild or domestic animals; the situation is significant—'these hard pan areas fringe the black cotton soils of the "mbugas" (valley grasslands)'—for, as mentioned above, it is in similar places that the bad effects of over-grazing and trampling by cattle are most evident in the Lake Kyoga basin. Milne (1936) has pointed out the difficulty of explaining the distribution and the composition of these 'hard pan' soils on the basis of parent rock and of climate, so it is probable that biological factors are also involved.

In *Bio-Ecology* Clements & Shelford state that 'the plant-animal formation is the basic community unit'. On this basis it may be said that the thicket growth, which is maintained in Karamoja when there is a large population of cattle, is a true climax and that the invasion of tsetse fly is a disturbance; but tsetse flies are indigenous to Africa, while cattle are not. It is also stated that 'At the most primitive levels, human families and societies are merely integral parts of the biome. It was only with the advent of agriculture and the control of the habitat by culture and especially of urbanization that man achieves such mastery of biome and habitat as to become an outstanding dominant of a new order. Such dominance, however, is chiefly the consequence of the development of steel and machinery. In pastoral areas, man perhaps is still to be reckoned as a constituent of the biome rather than the superdominant in it' (p. 24). This statement requires modification when the case of Karamoja is considered: for the Karamojong are not at the most primitive levels, yet they most certainly are not mechanized.

Bio-Ecology is founded largely on the ecology of temperate North America, about which a considerable amount is known; many of the principles apply equally to the ecology of tropical Africa, about which very little is known. Grazing, by inducing grasses with a bunchy habit, has the same effect in both temperate America and tropical Africa and so does overgrazing, by inducing bare ground and annual grasses; even some of the species, notably *Cynodon dactylon* and *Aristida adscensionis*, occur in both continents on overgrazed grasslands. The most spectacular example of the correlation between a solar cycle and biological phenomena is that of the swarming of locusts in tropical and subtropical countries.

Some of the details, however, need alteration if they are to conform to tropical African ecology. The action of animals in packing the soil is mentioned, but it is obvious that the effect could not be so marked in a temperate country, where the soil is subject to the disintegrating effect of freezing and thawing, as in a country where frost is unknown. The statement of Rush is quoted: 'Under ordinary conditions parasitic infections of wild animals are not yet serious; it is only when animals are concentrated under unfavourable conditions that the parasites, figuratively speaking, get the upper hand.' This statement is not in conformity with the effects of rinderpest on wild animals in tropical Africa; huge populations have been reduced to a few individuals and some species have been exterminated in many localities; domestic animals also have suffered intensely and the pastoral peoples, who were dependent on them for food, have died in large numbers from famine.

Clements & Shelford refer to the concentration of nitrates in the soil near the burrows of animals. In few parts of the temperate regions are animal burrows as extensive as those of termites in the tropics; there is an abundance of references to the termite as a destructive animal, but until recently little attention has been paid to its action in building up soil fertility: this action is localized and produces more striking results than that of earthworms in temperate countries.

Milne (1936) drew attention to the accumulation of bases in termite mounds, pointing out that the core of some mounds consisted of a hard concretionary mass of impure limestone, and discussing the physical and biological factors which might produce this result.

It has been found in Ceylon that in some cases the soil of termite mounds is richer than that of the adjoining soil and in some cases it is poorer (Joachim & Kandiak, 1940). In Thailand the soil of termite mounds has been found to have a much higher content of exchangeable bases than in the normal soil, and this increase of plant nutrients has a great influence on the growth of woody plants and on native agriculture (Pendleton, 1942). Similarly, in parts of Uganda where the soils are very poor, the growth of trees and shrubs may be confined to termite mounds (Thomas, 1941) and *Chlorophora excelsa* Benth & Hook., the most important timber tree in the Protectorate, is often associated with termite mounds and house sites, situations where there is an accumulation of bases (Thomas, 1942). The concentration of exchangeable bases on mounds may stimulate the growth of some plants, such as tobacco and retard that of others, such as tea; as mentioned above, these mounds may be valuable as 'licks' to augment the mineral supply of grazing animals.

Termites are abundant in Karamoja; some build mounds which are tall, like chimneys, and seem to serve the same purpose, for the air which rises from them is perceptibly hot to the hand. The amount of carbohydrates consumed to produce so much heat must be very considerable, and it is not surprising that there should be a marked concentration of minerals left as a residue from the plant materials eaten by the termites. Other species, whose nests are less spectacular, are yet exceedingly numerous and soon devour any dead wood which falls on the ground; they also attack living plants, making runs up the stems of many trees; and they do considerable damage to the soil cover by destroying tufts of grass. To the credit of the termites it must be stated that the runs underground greatly help the percolation of water and the runs on the surface must greatly impede the run-off, allowing more time for rain to sink into the soil. Little is known about the biology of the different species of termites in tropical Africa; a study of the subject would be difficult, but might be of great economic value in relation to agriculture.

In North America, before the advent of Europeans, the large herds of bison may have kept the cover of the plains as short grass (Larson, 1940). Similarly, in tropical Africa the abundance of herbivores has a great influence on the vegetation; the influence of domestic animals has been stressed in this paper, but the thousands of wild mammals in Karamoja must also produce great effects. In the grasslands and woodlands of the plains there are large herds of antelopes and zebra which graze the grasses; giraffe are abundant and browse on the trees; warthog are common and must have an important influence on vegetation and soil on account of all the plants which they root up; ant-bears and pangolins make burrows deep into the ground, throwing up large quantities of subsoil. Buffalo are abundant on the slopes of the mountains; there are large herds of elephants in the north-east of the district; rhinoceros are numerous in the Timu Forest; and in the thickets of the east the dik-dik, a miniature antelope, is very common. In spite of the numbers of these wild animals, their influence does not seem so important as that of the domestic flocks and herds. But overgrazing can be seen in parts of East Africa where there is no domestic stock; degradation of valley grasslands, such as is produced by domestic animals in eastern Karamoja, in places where the grasses are replaced by *Triumphetta flavescens* and *Abutilon guineense*, may be seen in the south-east corner of the Anglo-Egyptian Sudan and near the Ngorogoro Crater, Tanganyika, localities where there are annual migrations of enormous herds of antelopes.

Little is known about the causes and effects of these migrations of antelopes in Africa. Little is known about the migrations of elephants or of their effects on the vegetation; it has been suggested that they may be responsible in part for the peculiar distribution of *Borassus aethiopium* Mart. in well-defined belts, but it is probable that human agency is also involved. The cumulative effect of the browsing habit of elephants on African vegetation must be very great; this deforesting effect may be strikingly seen in the Gulu elephant sanctuary which lies on the banks of the Nile, about 100 miles to the west of Karamoja, an area from which the population was evacuated 30 years ago on account of sleeping sickness. In this sanctuary there are wide stretches of almost treeless grassland and with little or no regeneration of tree growth in spite of an abundant rainfall; for most of the smaller trees are browsed back heavily and many are knocked down by the elephants in order that they may feed more easily; even the bark of the larger trees, whose branches are out of their reach, is scored by their tusks.

Little is known about the coaction of wild animals on each other or of the reasons why widely diverse species tend to graze together and to migrate together. The balance between carnivores and herbivores may be easily upset, with striking consequences, as has been seen in Kenya where reduction of the numbers of lions has led to such an increase of zebra that they have become a major pest. The coactions between man and animals in tropical Africa are far from being understood; many species of birds are more abundant near human settlements than at a distance from them—probably for reasons of food supply. Similarly, antelopes often congregate near the grazing grounds of domestic stock, as they prefer the short tufted grasses to the tall erect species of ungrazed grassland; this phenomenon also may be seen in the Gulu elephant sanctuary where the grass of the uninhabited areas, 3 m. high when fully grown, is almost deserted of antelopes, while there are large herds of them on the grazing lands near the settlements on the edge of the sanctuary. Man certainly is an important member of the biome in Africa; human settlement is not, as might be imagined, solely antipathic to the increase of wild animals; the pastoral tribes, by controlled burning, produce flushes of grass which benefit not only their stock, but also the wild animals as well.

In spite of all that has been written about the influence of man on vegetation and soil in the tropics, the reactions are far from being fully understood and the magnitude of their cumulative effects is seldom realized. Studies of the prehistory of tropical East Africa are not of long standing, but the results already achieved demonstrate the existence of a diversity of Stone Age cultures and a density of settlement far exceeding that of corresponding cultures in temperate countries such as Britain. Even in Karamoja there was a distinct Mesolithic industry, the Magosian, named from a silted-up waterhole or granite cistern site at Magosi. Human settlement, extending over a period of thousands of years, is bound to produce great effects on vegetation and soil.

There has been a tendency to assume that, because an area was not inhabited at the end of the nineteenth century when the Europeans first came to East Africa, therefore it had never been inhabited; such a notion would be completely false, for it is obvious that there have been vast fluctuations in the populations of many parts of East Africa, fluctuations due to wars, disease, famines and migrations. Under European rule the calamities of war, disease and famine have been greatly reduced and the tribal migrations have been slowed down; therefore the populations have tended to increase and to remain settled on the same land, producing an increased pressure on the soil. Of recent years, the introduction of cash crops, grown for export, into the agriculture of communities which had been self-contained and self-sufficing, except for a little barter with their neighbours, has accelerated the changes and the degradation of soil and vegetation. Biological processes are rapid in the tropics, and the biological aspects of plant and animal ecology demand study, not only on account of their scientific interest, but also on account of their economic value and the necessity for more accurate knowledge before the tropical territories may be rightly developed.

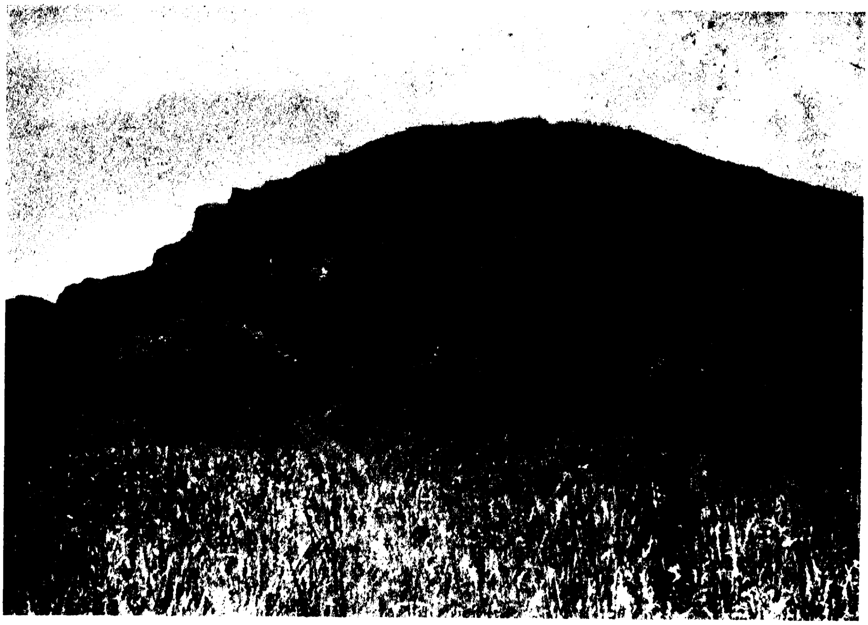
Summary

1. A brief description is given of the topography, soils and pastoral inhabitants of Karamoja, a large district in the north-east of Uganda.

2. The plant communities of the district and their more important constituents are enumerated. In short, these communities consist of open grassland on the plains in the south and west and of woodland around the mountains; near the centres of settlement in the east, the grasslands and woodlands are replaced by thickets. The zones of vegetation on the mountains are described as woodlands, forests, shrubby moorland and grassy moorland.

3. It is pointed out that the rainfall of the open plains, where grasses are the dominant plants, is less than that of the eastern valleys where the thickets are dominated by deciduous shrubs, many of which are very thorny, and by succulent plants.

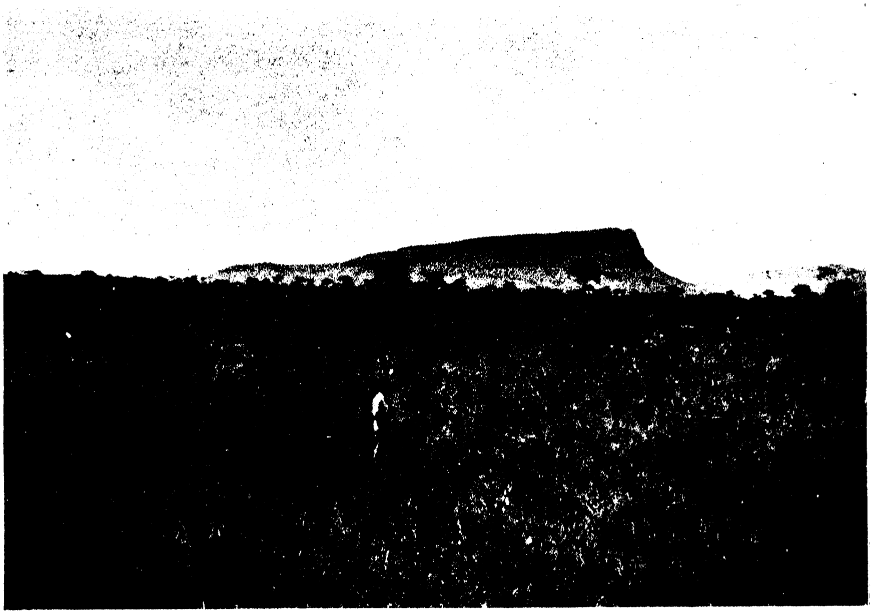
4. The influence of settlement, cultivation and grazing on the vegetation and the soil are discussed. The surface of the soil in the thickets has been so compacted by the trampling of animals that water cannot penetrate and, in spite of the considerable rainfall, the plants are growing under very dry conditions; therefore it is not surprising that the



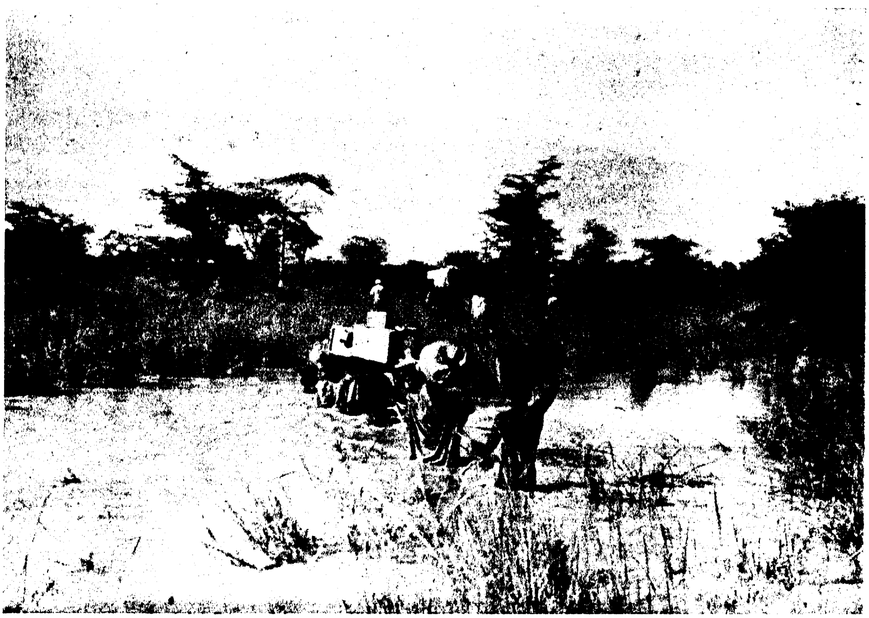
Phot. 1. Grassland west of Napak, heavily grazed in the dry season, photographed during the rains. *Hyparrhenia dissoluta*, *H. rufa*, *Themeda triandra* and *Setaria sphacelata* are common grasses.

Phot. 2. Open woodland south-west of Napak, ungrazed. The most common trees are *Combretum binderianum* and *C. Gueinzii*; the most common grasses are *Hyparrhenia dissoluta*, *H. filipendula*, *H. rufa*, *Setaria sphacelata*, and *Themeda triandra*.

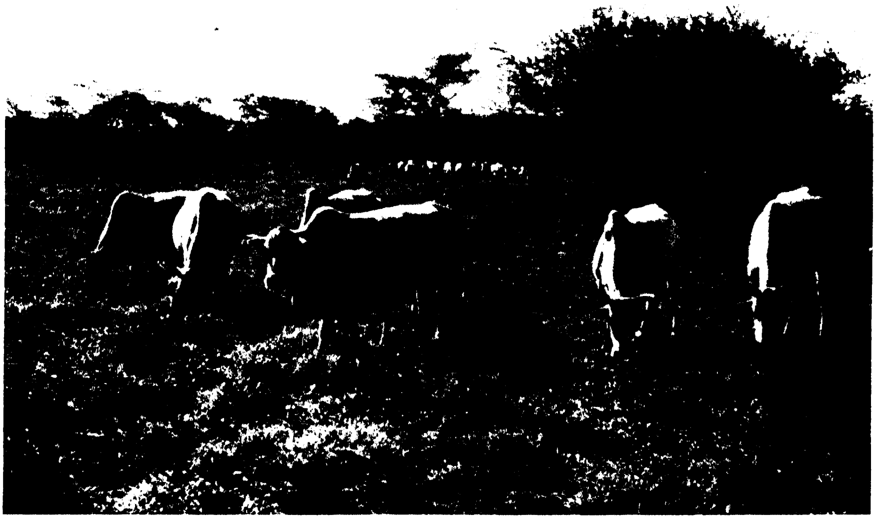
Phot. 3. Exposed rock moss on the Labwor Hills; *Vellozia* sp. dominant.



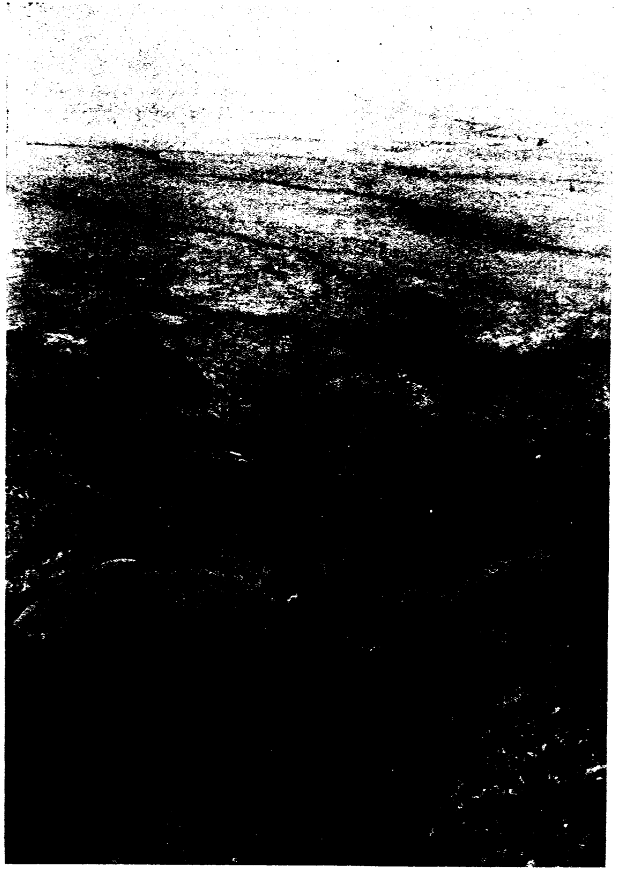
Phot. 4. Valley grassland north of Napak, *Setaria Holstii* and *S. incrassata* are the common grasses; the small trees are *Acacia drepanolobium* and the few larger ones are *Balanites aegyptiaca*.



Phot. 5. Valley grassland north-east of Napak; the grasses are mostly *Setaria Holstii* and *S. incrassata*; the small trees are *Acacia drepanolobium* and the taller ones are *Acacia seyal* and *A. seyal* var. *fistula*.

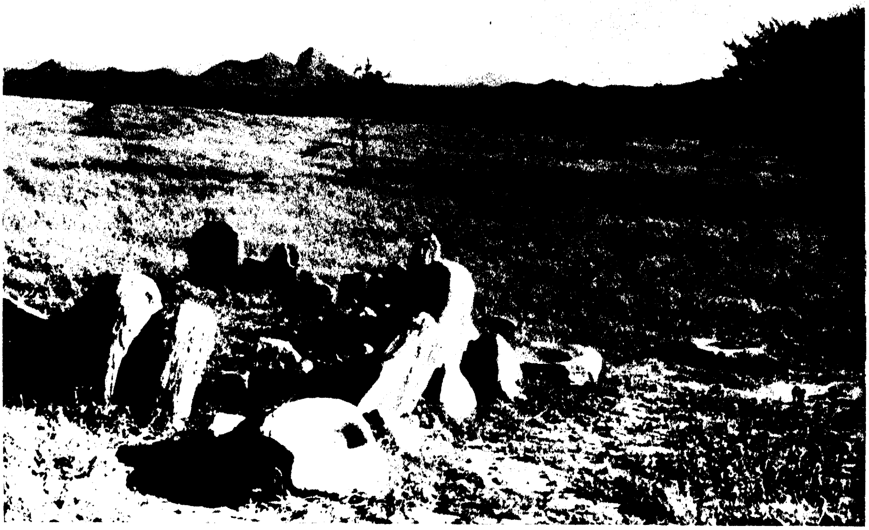


Phot. 6. Overgrazed grassland near Kangole. Short tufts of *Pennisetum ramosum* and *Chrysopogon aucheri* are common, but most of the ground cover is of *Barleria eranthemoides*. The nearest tree is *Acacia mellifera*; other *Acacia* spp. are in the background.

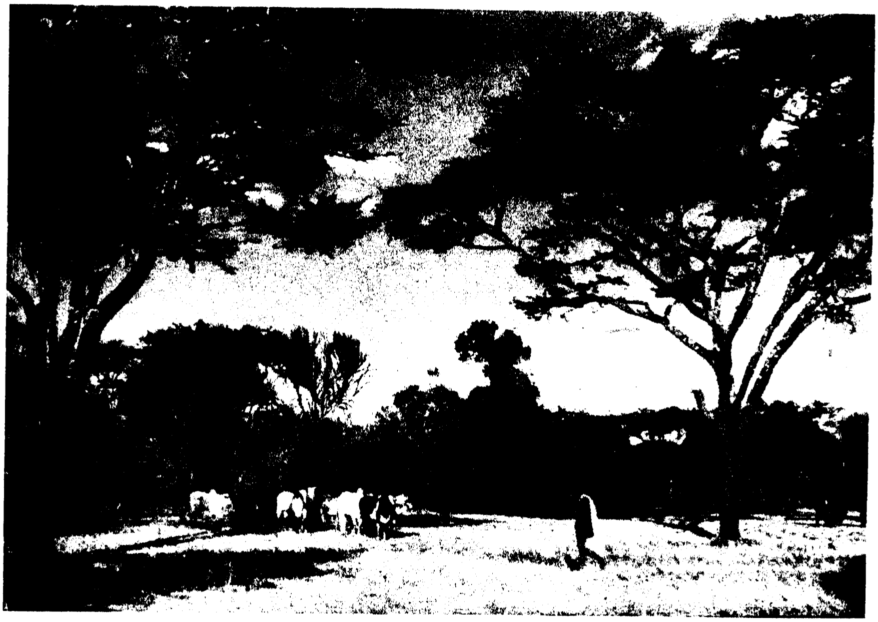


Phot. 7. A view down the western slopes of Moroto mountain showing the sparse cover of stunted shrubs and trees; the dark lines of riverain forest mark the watercourses across the plain.

Phot. 8. Woodland near the base of Kadam. *Combretum Gueinzii* is the dominant tree; *Hyparrhenia dissoluta*, *Themeda triandra* and *Setaria sphacelata* are common grasses.



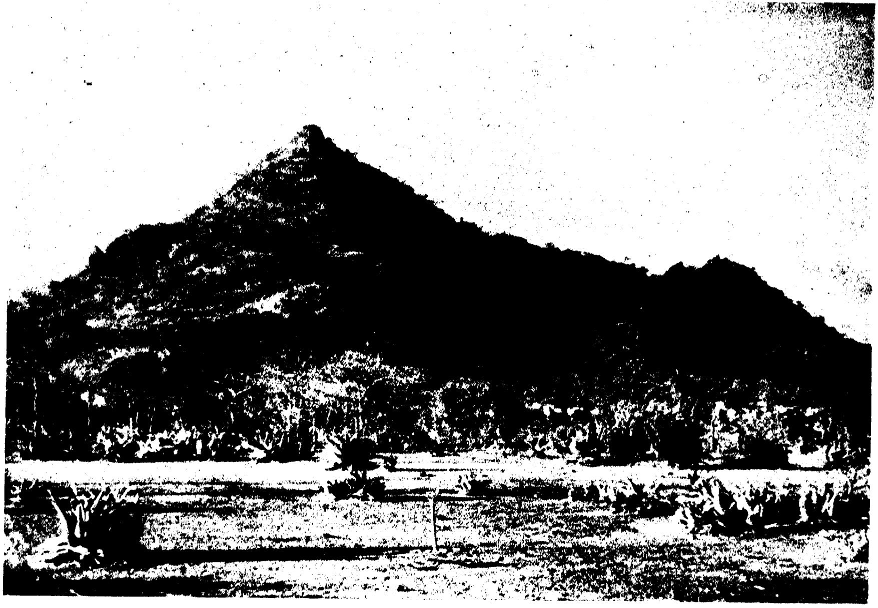
Phot. 9. A hill-top near Loyoro covered with grassland in which *Cynodon plectostachyum* is dominant. In the foreground are some grindstones and a stone-hut circle, relics of former agricultural peoples.



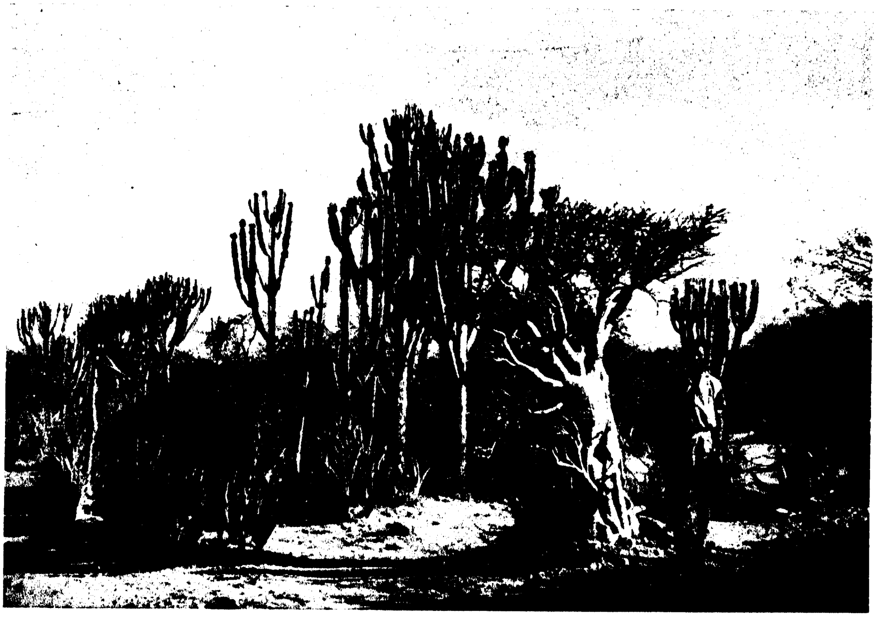
Phot. 10. A valley in the Timu Forest. The nearest trees are *Acacia hebecladoides*; other *Acacia* spp. and *Euphorbia calycina* beyond. The grasses are *Themeda triandra*, *Sporobolus pyramidalis*, *Chloris gayana* and *Cynodon plectostachyum*.

Phot. 11. Acacia woodland near Moroto: *Acacia tortilis* and other *Acacia* spp. and *Euphorbia calycina*.

Phot. 12. Deciduous thicket near Loyoro; *Acacia orfota* and other *Acacia* spp.



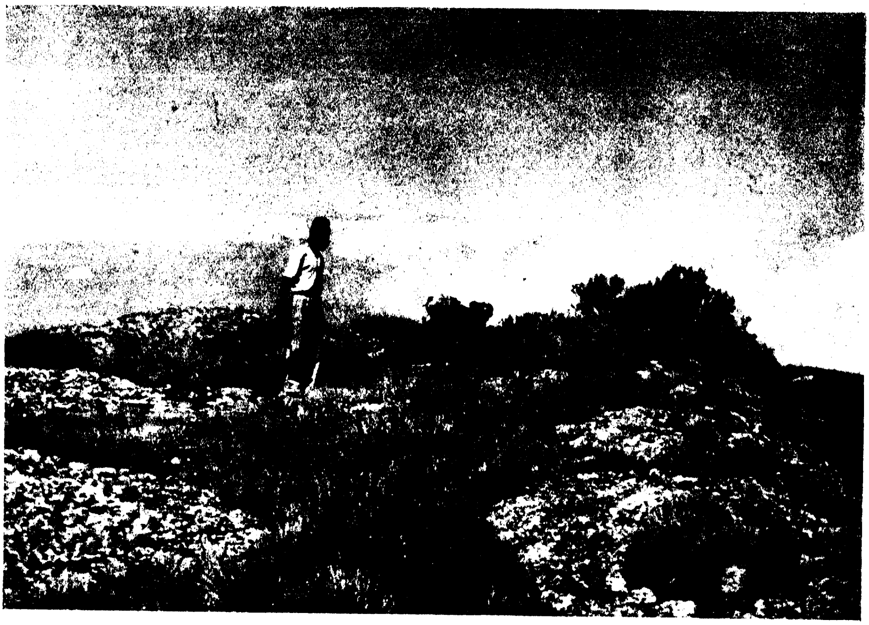
Phot. 13. Deciduous thicket near Loyoro: bare ground with clumps of *Aloe* sp. and *Sansevieria Ehrenbergii*; behind is a thicket of *Lannea* spp. and *Commiphora* spp., while *Acacia pennata* is dominant on the hill.



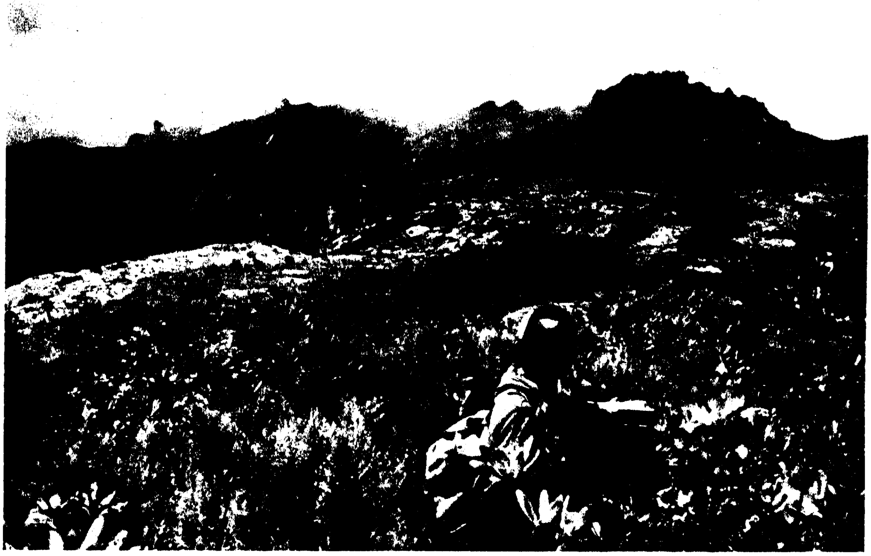
Phot. 14. Succulent thicket near Loyoro: *Adenium Honghel*, *Euphorbia calycina*, *Sansevieria Thunbergii* and *Aloe* sp.

Phot. 15. Forest on the slopes of Kadam, and the steep cliffs which surround the plateau at the summit.

Phot. 16. Woodland on the slopes of Napak: *Combretum* spp. and *Terminalia* spp. are the most common trees. *Hyparrhenia filipendula*, *Setaria sphacelata* and *Themeda triandra* are common grasses.



Phot. 17. Grass moorland on thin soil over rocks near the summit of Kadam; *Eragrostis lasiantha* is the dominant species in this patch.



Phot. 18. Shrubby moorland near the summit of Kadam; *Protea abyssinica* and *Erica aborea* are codominant.

dominant species are xerophilous. In addition to the physical effect of compaction, the chemical effect of the concentration of plant nutrients is mentioned; the distribution of some species typical of Karamoja thickets appears to be influenced by the concentration of bases in the soil.

5. Biological factors in relation to the ecology of tropical Africa are discussed, especially in relation to the effects of termites, of game animals and of man; little is known about the interaction of these factors and of the magnitude of their cumulative effects.

Grateful acknowledgement is paid to the Staff of the Herbarium at the Royal Botanic Gardens, Kew, and to Mr P. J. Greenway, Systematic Botanist, Amani, for the determination of plants collected.

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STUDIES IN THE AUTECOLOGY OF *ASCOPHYLLUM NODOSUM* LE JOL.

By HAROLD M. DAVID

(*With Plate* 12 *and five Figures in the Text*)

From 1937 to 1942 an ecological survey was carried out on the intertidal algae in Aberystwyth Bay. In this bay three rocky promontories take their names from well-known landmarks. From north to south these are: Constitution Hill rocks, Queen's Hotel rocks and College rocks (Pwll Padarn) (Fig. 1). Owing to the configuration of the coast the amount of shelter these rocks receive increases from north to south of the bay.

During the course of this investigation particular attention was directed to problems of recolonization in certain areas and also to the study of *Ascophyllum nodosum* Le Jol. in view of its abundance and the luxuriance of growth in the consociation which it forms.

Although in the considerable literature (Cotton, 1912; Delf, 1932; Gibb, 1939; Johnson & Skutch, 1928; Lyle, 1920; Rees, 1931, 1932) on the ecology of *Ascophyllum* it is reported that this alga occurs in both sheltered and exposed localities wherever the substratum affords good anchorage, yet in the Aberystwyth bay, *Ascophyllum* grows most abundantly on the inner and comparatively sheltered part of College rocks, occurring less frequently on the more exposed rocks to the north-east. Thus, although the optimum conditions of growth of *A. nodosum* have never been clearly defined, judging by the wealth of the *Ascophyllum* flora on the College rocks and the conditions obtaining there, the evidence at Aberystwyth suggests that, in Cardigan Bay, *Ascophyllum* prefers comparative shelter. Prevalent winds here are, of course, westerly.

The distribution of other intertidal algae, e.g. *Porphyra umbilicalis* f. *linearis*, is undoubtedly influenced by the entry of sewage-bearing river water and hence it cannot be overlooked that the proximity of the College rocks to the mouths of the rivers Rheidol and Ystwyth may indicate that the distribution of *Ascophyllum* could also be correlated with the incoming river water and with observed variations in the chemical composition of the waters of the bay.

The tidal range for the Aberystwyth shore is about 18½ ft. (5½ m.) during the extreme spring tides and about 5½ ft. (1·7 m.) during extreme neap tides giving a wide intertidal region of attached marine algae of approximately 250 yd. (229 m.).

The *Ascophyllum* consociation on the College rocks extends from the *Fucus spiralis* zone down to the *Fucus vesiculosus* zone, i.e. from E.L.H.W.N. down to E.H.L.W.N. (see p. 181). Whilst the vertical distribution is approximately 1·73 m., the horizontal distribution is particularly extensive owing to gentle slope, and covers 126 m. in a typical belt transect. Since the consociation is well-defined, having horizontal continuity and with a well-defined upper and lower limit, it is usually referred to as a zone.

The transition from the *F. spiralis* consociation to that of *Ascophyllum* is remarkably sharp. There is very little, if any, real mingling, for where the *Fucus spiralis* merges into the *Ascophyllum nodosum* zone the *Ascophyllum* is at a lower rock level. The sharp boundary between *Fucus spiralis* and *Ascophyllum* has been observed by many algologists.

Zaneveld (1937) attributes the sharp demarcation to the factors of desiccation, whereas Cotton (1912) maintains that the structure of the substratum is responsible. Colman (1933) states that there is 'some noxious influence on the part of one or other alga or of both'. The question of angle of slope, of course, cannot be overlooked.

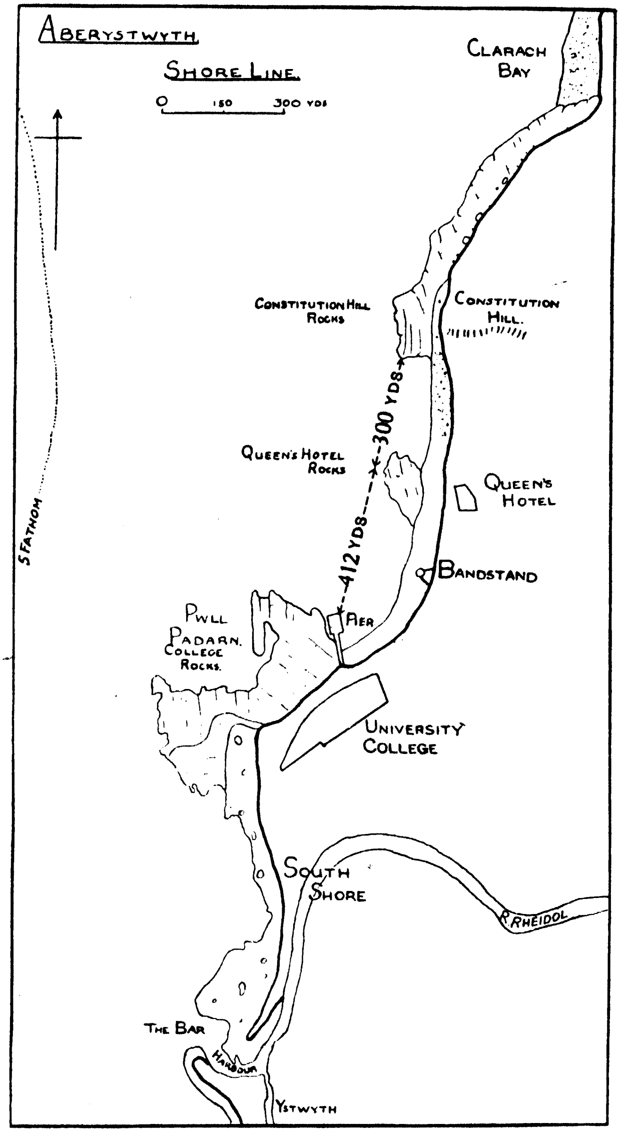

Fig. 1. Aberystwyth shoreline.

The lower limits of the *Ascophyllum* zone are less sharply defined. Towards the bottom of the zone, *Fucus vesiculosus* appears as an 'occasional' above E.H.L.W.N., where it occurs almost entirely as an epiphyte on the *Ascophyllum*. Presumably the *Fucus vesiculosus* plants could grow higher up on the College rocks at Aberystwyth, but are there crowded out by the *Ascophyllum* plants. On the Queen's Hotel and Constitution Hill rocks to the north of the bay the relative positions of *A. nodosum* and *Fucus vesiculosus* are interchanged, as Lyle records for the Guernsey coast (1920). These rocks to the north-east are subject to much more buffeting from the south-west gales than are the College rocks, and the *Ascophyllum* thalli do not attain the same length on the more exposed rocks. It would appear that in this, as in other zones, size of plants may prove to be important in determining zonal positions.

The *Ascophyllum* zone may conveniently be subdivided into three parts:

(1) The upper (or top), from M.H.W.N. down to E.L.H.W.N.
(2) The middle, from E.L.H.W.N. down to M.S.L.
(3) The lower (or bottom), from M.S.L. down to E.H.L.W.N.

This subdivision delimits that central part of the zone in which *Ascophyllum* grows most luxuriantly.

The behaviour of the tide during its ebb and flow is both unusual and interesting. It probably accounts, to a great extent, for the width of the zone. When measured on a vertical tide gauge it can be seen that the tide flows evenly for 2 hr., then much faster and over a greater vertical distance during the next 2 hr. and then slowly up to the full tide. There is a similar difference in the rate at which the tide ebbs after reaching the full. During the middle two-hourly period of a neap tide the *Ascophyllum* zone is completely covered or uncovered. On a spring tide, however, the water takes less than 2 hr. to flow over the *Ascophyllum* zone. That the increased area exposed during the middle two-hourly period is due to the rapid rise, or fall, in the height of the tide and is not due primarily to a gradually shelving shore can be shown by plotting the tidal range of spring and neap tides in relation to the height above and below mean sea level (M.S.L.) (Fig. 2).

Another feature of interest relating to the relative force of the current in the ebb and flow is the constancy of the direction of the lie of all the larger brown algae during the period of exposure. The thalli of *Ascophyllum* when exposed during the ebb tide lie in the direction of the inflowing waves. This was true during both neap and spring tides and also during south-west and north-east gales. Thus the incoming waves, even during gales, must produce a stronger flow of water than the ebb current.

THE NATURE OF THE BRANCHING, GROWTH, REPRODUCTION AND REGENERATION IN *ASCOPHYLLUM NODOSUM*

In *A. nodosum* the main thallus is compressed and often dichotomously branched. All except the oldest parts of the thalli bear short, young shoots laterally and mostly in tufts. Each young shoot in the distal regions of the older plants may develop into either a receptacle, terminal on a short receptacle branch, or grow out into a branch resembling an arm of the main dichotomous vegetative branch. Such branches develop either at the bases of young plants, or when the apical portion of an older plant is injured or cut away; in either case growth and reproduction is carried on by these lateral branch outgrowths.

Regeneration and Branching

The whole subject of regeneration in the Fucales is rather obscure. Whilst some Fuci, for example *Fucus spiralis* and *F. vesiculosus*, seem to regenerate more readily than others, e.g. *F. serratus*, *Ascophyllum nodosum* shows frequent regeneration from both holdfast and fronds. There is a good deal of variation in any one species, and observation suggests that certain individuals are more prone to regeneration than others. When the thalli of *Ascophyllum* plants in ½ m. quadrats were severed artificially below the region which bore receptacles, no regeneration occurred from the cut surfaces. If, however, the thalli were severed, either artificially or by wave action, above this region, one or more new laterals frequently grew out from the pits which normally bore receptacles. This seemed to be true of all *Ascophyllum* plants up to five years old. Very old plants appeared to have lost the power of regeneration altogether. In the sporeling stage of the plants the lateral meristems, so familiar in the later growth regions, were not present. To the absence of these meristems must therefore be attributed the lack of ability to regenerate in the proximal regions of the plants.

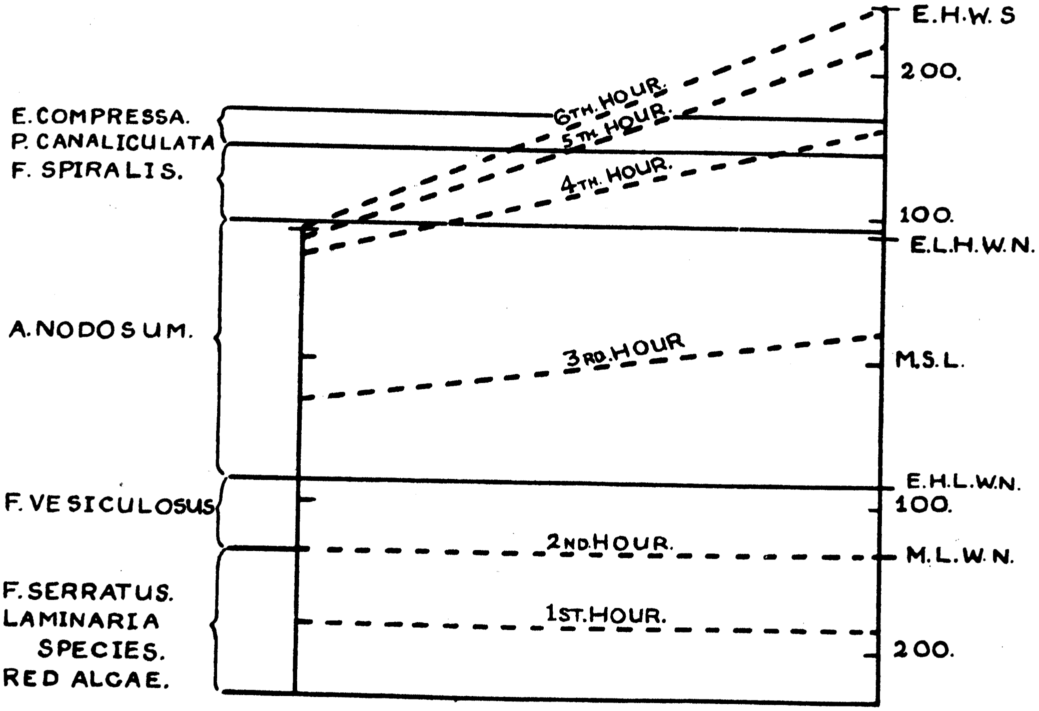

Fig. 2. Tidal ranges and zonation, Aberystwyth.

Tidal data for Aberystwyth

Extreme high-water Springs (E.H.W.S.)	+247·5 cm.
Mean high-water Springs (M.H.W.S.)	+228·6 cm.
Mean high-water Neaps (M.H.W.N.)	+119·5 cm.
Extreme (lowest) high-water Neaps (E.L.H.W.N.)	+ 89·0 cm.
Mean sea-level (M.S.L.)	0
Extreme (highest) low-water Neaps (E.H.L.W.N.)	− 84·7 cm.
Mean low-water Neaps (M.L.W.N.)	−132·3 cm.
Mean low-water Springs (M.L.W.S.)	−255·4 cm.
Extreme low-water Springs (E.L.W.S.)	−319·4 cm.
M.S.L. Ordnance Datum = height above Chart Datum,	261·5 cm.

The main branching systems of *A. nodosum* are monopodial, dichotomous and its modification trichotomous (Pl. 12, fig. 1). In order to see whether there was any correlation between mode of branching and the distribution or habitat of the plants in the zone some 300–400 plants were examined from each of six different localities:

Plants growing on rocks at the top of the *Ascophyllum* zone.
Plants growing in pools at the top of the *Ascophyllum* zone.
Plants growing on rocks in the middle of the *Ascophyllum* zone.
Plants growing in pools in the middle of the *Ascophyllum* zone.
Plants growing on rocks at the bottom of the *Ascophyllum* zone.
Plants growing in pools at the bottom of the *Ascophyllum* zone.

	Monopodial branching		Dichotomous branching		Trichotomous branching	
	Rock %	Pool %	Rock %	Pool %	Rock %	Pool %
Top	71	63·5	28	32·5	1	4
Middle	91	76	9	23	—	1
Bottom	76	62	21	36	3	2

The only conclusion drawn from this table is that there appears to be more monopodial growth in plants in the middle of the zone than at the extremities. This may be associated with the greater length of the thalli in this region of the *Ascophyllum* zone. Plants from rock pools show a greater percentage of dichotomies than those on the neighbouring rocks. The number of plants showing trichotomy was too small to allow of any conclusion being drawn. Any of these systems may bear secondary lateral branches. In a few abnormal plants a great deal of regeneration occurred, and the newly developed branches did not conform to any of the above-mentioned branching systems.

In her short paper on the annual growth of *A. nodosum* MacFarlane (1930–8) refers to the normal dichotomy of the branches after the production of the main air-bladders. It would appear that the plants of *A. nodosum* may well behave differently in Canadian seas, for examination of a large number of marked plants at Aberystwyth shows that the greater number of branches are monopodial and do not dichotomize at all, though producing normally a single air-bladder per year, as is explained later (Pl. 12, fig. 2).

Experimental removal of receptacles. Receptacle branches were removed artificially in January 1939 from fifty male and fifty female plants in 3 sq. m. situated respectively at the top, middle and bottom of the zone. In January the receptacles were young and it was thought that new receptacles might develop, as Oltmanns (1922) suggests, and fruit at the normal time. There was, of course, another possibility, that new lateral vegetative branches would grow out and that these would develop receptacles during the following year (1940). The first signs of regeneration appeared in May 1939, the plants in the middle of the zone showing at any time more advanced regeneration than those at the extremities of distribution. Though these new outgrowths grew and were about 2 cm. long at the time when the remainder of the plants were exuding gametes (April–May), there were no signs of receptacles being developed on these lateral outgrowths until November and December (1939). At this time new receptacles were also developing on the rest of the plants in the zone for the production of gametes in the following year (1940). Thus, by removing the receptacles during their early development the plants do not form sex cells during that season. These plants were kept under observation until 1942 in order to see whether there would be produced a greater abundance of receptacles than on the control plants, but no difference was observed. It is not known whether removal of the receptacles at an even earlier age would lead to a second crop developing in any one season or whether any effect on the crop of receptacles in a subsequent season could be initiated by removal of maturer receptacles. It is possible that this artificial removal of the young receptacles may have served to prolong the life of these particular plants in somewhat the same way as the vegetative life of an ephemeral flowering plant, like chickweed, under controlled conditions, may be prolonged by removing the flower-buds as they appear.

The reproductive and vegetative periods tabulated below have been observed during four consecutive years on plants growing at Aberystwyth. Data for *Ascophyllum* collected from other parts of Great Britain and North Brittany are almost identical.

Reproductive and vegetative growth phases of Ascophyllum nodosum *Le Jol. during the year*

Month	Reproduction	Vegetative growth
End of May June	First appearance of lateral outgrowths (young receptacle branches)	—
October	Appearance of conceptacles	New vegetative growth initiated at apex shows only slight elongation during late autumn and winter
November	—	—
December	—	—
January	First visible signs of sperms and cleavage walls in oogonia	—
February	Dehiscence—rarely—end of February	—
March	—	First signs of air-bladder formation
April	Max. dehiscence of gametes. Exfoliation of receptacles begins	Air-bladder formation complete
May	Max. exfoliation of receptacles	Continued apical growth after air-bladder formation

Growth

Growth in *Ascophyllum nodosum*, as in all other members of the Fucaceae, is apical. Oltmanns (1922) maintains that *Ascophyllum* is peculiar in that, in the young plants at the apex, a number of little secondary pits arise on either side of the apical cell. These pits are not exactly opposite nor yet alternate. At the base of each pit a four-sided cell, like the apical cell, divides into twelve apical cells each of which can give rise to a lateral shoot. Most of these cells normally remain quiescent, three or four only grow out into either a main lateral branch or into three or four receptacle branches.

The first sign of new seasonal growth observed each year was the appearance of whitish tips to the thallus branches about mid-October. It will be shown that, after the initiation of this new growth, little elongation of the thallus took place until after the receptacles had reached an advanced stage of development and, in some instances, until after dehiscence had taken place. The explanation of this retardation of elongation may possibly be found in low rates of metabolism during the lower temperatures of late autumn and winter. Alternatively, it may be that the production of receptacles uses up the foodstore of the previous year during their formation as well as any assimilate produced during the winter. These whitish tips were always visible first towards the top of the zone and later progressively downshore.

During March a slight swelling appeared in this new growth region right at the apex. This swelling expanded into a new air-bladder with signs of further apical growth above the bladder in about one month. Similar observations were made on plants in other parts of Cardigan Bay, and it is likely that all plants in the British Isles behave somewhat similarly.

By counting the bladders on thirty marked plants from November 1938 to October 1940 throughout the zone it was ascertained that only one air-bladder was normally produced annually on a monopodial thallus or on an arm of a dichotomously or trichotomously branched thallus (Pl. 12, fig. 1). Apart from this normal bladder formation an additional air-bladder may be formed as a result of injury to the single annual bladder and also, exceptionally, on the receptacle branch (Pl. 12, fig. 4).

During the period of marked apical elongation (April to October) upwards of five or six receptacle pits were laid down on either side of the enlarging apex of each plant, but only the proximal one or two meristems near the last-formed bladder grew out into receptacle branches in the following reproductive period (October 1939–May 1940). The remaining meristematic regions nearer to the apex did not give rise to receptacles until the second reproductive season after they had been laid down. Persistent meristems from growth of two, three or more earlier seasons also gave rise to additional receptacle branches. It was this distal region of the thallus which provided the fertile receptacles each season, the older proximal region below and that above the first-formed bladder remaining sterile. Thus, in a plant six or seven years old, during the fruiting season that portion formed during the first two or three years bore no receptacles, neither did that of the first four or five years in a ten-year-old plant.

There was a greater number of receptacles occurring in the middle of any one reproductive region on a frond than above or below this region.

The occurrence of the receptacle-branch meristems laterally and at approximately equal distances apart, so as to appear almost opposite in arrangement, suggests a rhythm in their production. It is possible that somewhat similar factors operate in the production of these meristems as at the apical meristems of a flowering plant producing leaf primordia.

The greater number of receptacles in the middle of the thallus is to be correlated with the greater activity of the meristems in the lateral pits, but whether this greater activity in the middle of the thallus can be maintained throughout the life of the plant, or whether it is limited by the number (frequently twelve) of meristematic cells laid down in the young stage of the development at the apex, is not known. Perhaps the meristematic cells have been used up in the oldest part of the reproductive region of the thallus, and that only one or two have reached maturity in the youngest part of the thallus distal to the last-formed air-bladder. A period of about twelve months elapses after these 'nodal' pits have been laid down before the majority of the lateral receptacle branches begin to appear. It seems feasible to assume therefore that the 'nodes' which had been laid down for a longer period (2–5 years) should produce a greater number of receptacles because they have been in existence longer and because the varied factors determining the activity and development of the meristematic initials have caused more receptacles to be produced. Further, a meristematic cell is used up completely in the production of a receptacle branch, so there would be fewer meristematic cells left in the oldest 'nodes' to give rise to additional receptacle branches. The literature provides no data as to the length of time the unused meristematic cells may remain active in these 'nodal' cavities, but evidence from 'experiments on injury' showed that regeneration took place from 'nodes' known to be five years old, and examination of plants on the shore showed that, occasionally, regeneration took place from even older 'nodes'. It is exceptional for 'nodes' more than five years old to give rise to receptacle branches.

Examination of any one thallus also showed that the 'internodes' were longer in the middle of the thallus than in the proximal and distal regions. If a comparison with the internodes of the higher plants is made, it is noticed that here, too, the youngest and oldest internodes are the shortest.

In most thalli over three or four years old three marked colour zones could be differentiated: (*a*) a dark brown or blackish zone at the base, (*b*) a brown middle zone, and (*c*) a yellowish zone which was the youngest portion of the thallus.

Variation in size of air-bladders

The production of air-bladders seemed to be, for the most part, caused by a separation of the medullary hyphae, the limiting and cortical layers not being markedly affected. Therefore the meristematic 'nodes' which penetrate the cortical layers only were not affected by the formation of air-bladders. Bladder formation was not always 'internodal', i.e. between the receptacle pits, but sometimes involved a lateral 'node' or 'nodes' (Pl. 12, fig. 4).

The first-formed and the last-formed bladders on any thallus were always smaller than those in the central region of the thallus. By displacement of sea water, the volume of 100 bladders from each of thirty plants from top, middle and bottom of the zone showed that not only are the bladders of *Ascophyllum* plants larger in the middle of each thallus but also that the bladders on individual thalli of plants in the middle of the zone were larger than corresponding air-bladders at the bottom of the zone and these latter were larger than the air-bladders on thalli at the top of the zone. Some of the largest bladders taken from plants growing in the middle of the zone were three or four times the size of the largest bladders to be found in other parts of the zone. The presence of such large bladders can no doubt be correlated with the luxuriance of growth in the middle zone. As to the gaseous contents of the air-bladders, Damant (1937) maintains that plants of *A. nodosum* exposed to severe hydrostatic pressure have thickened bladder walls which enable them to resist deformation, but that there may be a disastrous loss of gas during an abnormally high tide and the bladders would then no longer be able to support the plant which may thus become damaged permanently. Damant also states that 'the gas in the bladders from October to December is chemically equivalent to air; for the remainder of the year the percentage of oxygen increases'.

There appeared to be a succession in the formation of the air-vesicles and air-bladders in *Ascophyllum* and certain Fuci downshore. Their formation followed closely the onset of reproduction. In *A. nodosum* the first appearance of air-bladders normally occurred in early April, preceded upshore, early in January, by the formation of air-vesicles in *Fucus spiralis* and succeeded downshore by the air-bladders of *F. vesiculosus* early in May and, when formed, by the air-vesicles in *F. serratus* about the middle of May. It has been considered advisable to reserve the term 'air-bladder' for pneumatocysts of definite shape and the term 'air-vesicle' for those which have no definite shape.

Reproduction

While sexual reproduction of *Ascophyllum* plants takes place, in general, during the same months of the year throughout the British Isles, it would appear from specimens collected from various localities along the coast of Britain, that reproduction was slightly earlier along the south coast than on the colder Scottish coasts. The relationship between the apical growing points and the origin of receptacle branches has been described above. The first visible signs of the formation of conceptacles was observed during late October and early November. These early stages were distinguished by an enlarging of the apices of the receptacle branches which had been initiated in the previous May or June. These branches originated first on the plants at the top of the zone around the scars of former receptacle-branch stalks, presumably from the persistent lateral meristems already described. This earlier development on plants at the top of the zone was maintained throughout the later reproductive phases. There was a similar succession in development from the apex to the base of any individual plant. The factors determining this difference in time of development of the receptacles in different positions on the plants in the zone is not known. It is possible, however, that as Hyde (1938) showed for *Fucus serratus*, the 'apparent assimilation rate' increases with increasing light and temperature, so the greater amount of light and the more prolonged exposure to air temperatures which *Ascophyllum* plants receive in the upper regions of the zone may give rise to increased assimilation and food supply for these young growing parts. The disposition and amount of assimilatory tissue showed that most active assimilation took place in the younger portions of the thalli. Though the questions of translocation of the food stored in different regions of the *Ascophyllum* plant has not been studied, it may be significant that the region of earliest development of reproductive receptacles coincided with that part of the thallus where assimilation was most evident. It will be shown later that the average age of plants in the upper reaches of the zone was less than the average age of those growing lower down. Moreover, there is convincing evidence that the growth and vitality of plants growing in the lower reaches of the zone were affected by the parasitic *Polysiphonia fastigiata*. Hence, in the lower part of the zone, two additional factors affecting receptacle development come into operation, viz. the increasing age of the plants and the effects of the parasite.

The cause of the initiation of the reproductive receptacles has been a matter of speculation for some time. Farmer & Williams (1898) and, later, Baker & Blandford (1916), maintained that a certain limiting concentration of the cell sap is necessary as a stimulus for the production and maturation of sexual bodies, and that the formation of sexual organs becomes habitual after a preliminary series of stimuli. Further investigation may well show that *Ascophyllum nodosum*, like *Fucus spiralis* and *F. vesiculosus*, the receptacles of which are initiated at the onset of cold winter conditions, may receive some sexual stimulus controlled by a temperature factor, possibly involving a chemical change of food store, which is responsible for their peculiar behaviour. That this reproduction may be related to chemical changes in the sea water is not unlikely, and the rise in nitrate nitrogen and phosphate in the sea water, as shown by Harvey (1928), during their reproductive period may be an additional factor to be considered, especially since it is known that, in some of the higher plants, the attainment of a certain critical balance between carbohydrate and nitrogenous substances is necessary before reproduction will take place (Kraus & Kraybill, 1918). The recent work of Kuhn, Moewus and their collaborators on *Chlamydomonas* indicates that our knowledge of sexual processes in the algae and in other plants is as yet incomplete (Heilbron, 1942).

While the conceptacles were being differentiated in *Ascophyllum*, the receptacle branch widened at its apex into either an oval or rounded flattened disk. These disks later began to swell as the conceptacles became more mature. In view of this observation it was decided to attempt a measurement of this change in volume of the receptacles. Four typical healthy and uninjured plants were marked—one male plant from the top, middle and bottom of the zone, and, in addition, one female plant at the bottom. In order to make the observations on twenty receptacles from each plant, all the receptacles on both arms of one dichotomizing branch were measured. In view of the necessity of making repeated measurements on the same receptacles the period of observation had to be reduced to a minimum. Attempted observations over the whole period of development of the receptacles (October–May) had to be abandoned since some of the plants were dislodged or portions dismembered. In addition, predatory molluscs, such as *Littorina obtusata*, in search of their food supply, took their toll of some receptacles. It was decided, therefore, to observe the receptacles from February to May, this being the period of most marked swelling of the maturing receptacles prior to dehiscence. Here again the molluscs punctured some receptacles before all the gametes had matured and dehiscence had taken place. In spite of these difficulties a complete record of the length, width and thickness of many receptacles was obtained, the records for the injured receptacles being discontinued after injury had taken place (Fig. 3). In order to get some idea of the volume changes from the earliest stages in development to the time of exfoliation, 110 receptacles were collected periodically (weekly) from plants at the top and bottom of the zone and the total displacement measured. In choosing the receptacles all the receptacles from several thalli collected from the top and bottom of the zone were taken. The results of the estimations are shown in Table 1 and Fig. 4.

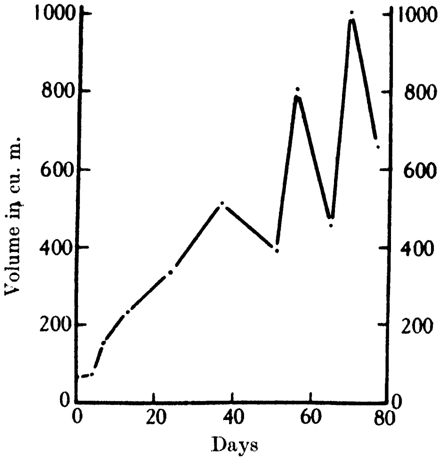

Fig. 3. *Ascophyllum nodosum* Le Jol. Graph to show increase in volume of a typical marked receptacle (one of 25 recorded *in situ*) over a period of 80 days, prior to and during dehiscence.

To obtain some measure of the volume from receptacles *in situ*, linear dimensions alone had to be utilized, the measurements being made on marked plants. By assuming the receptacles to be perfect ellipsoids a volume value was obtained. Experimental investigations showed that this volume calculation from linear dimensions may involve an error of ±3·5%, as compared with estimates by displacement. The results are not given in detail, though a typical example is shown in Fig. 3.

It was thus possible to obtain some comparison between the volume changes of individual receptacles as well as those of averages of a large number (110) of receptacles. In both cases, the results show the general increase in receptacle volume during spring. There are, however, also large fluctuations in volume in the mature receptacles (see Figs. 3, 4), and the analysis of results for individual marked receptacles (Fig. 3) shows that marked decreases in volume are associated with dehiscence of the conceptacles. The volume then

Table 1. Ascophyllum nodosum *Le Jol. Volume of* 110 *receptacles collected periodically from top and bottom of the zone, from the early stages of receptacle development until the end of the fruiting period (all figures + or* −3·5%)

Days	Date	Top of zone c.c.	Bottom of zone c.c.	Days	Date	Top of zone c.c.	Bottom of zone c.c.
	4. xi. 39	9	8	96	8. ii. 40	21	14
6	10. xi. 39	12	8	107	19. ii. 40	36	16
13	17. xi. 39	8	10	119	2. iii. 40	34	19
20	24. xi. 39	6	10	126	9. iii. 40	21	28
27	1. xii. 39	15	11	131	14. iii. 40	58	23
34	8. xii. 39	—	13	151	3. iv. 40	22	16
45	19. xii. 39	9	12	163	15. iv. 40	52	33
62	1. i. 40	11	10	173	25. iv. 40	74	43
73	16. i. 40	12	12	180	2. v. 40	61	46
79	22. i. 40	14	10	196	18. v. 40	38	45
88	31. i. 40	14	26	202	24. v. 40	—	42

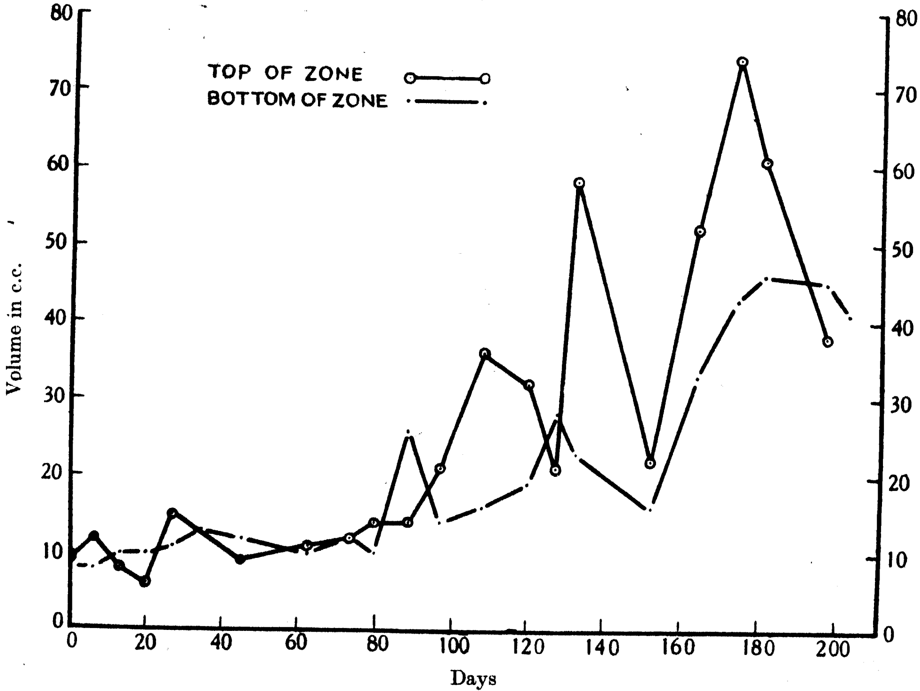

Fig. 4. *Ascophyllum nodosum* Le Jol. Graph to show average volume changes of 110 receptacles from plants at top and bottom of the zone. Over a period of 200 days including the period of dehiscence.

increases again to a still higher level, followed again by a subsequent marked decrease as further dehiscence takes place.

The decreases are caused, presumably, by the loss of gametes and mucilage and possibly of the absorbed water in the mucilage of the receptacles. Although the exact processes of dehiscence have never been described, most writers agree that the process is helped by the changes in water content of the mucilage in the receptacles during the intertidal period. It will be observed that the third maximum (Fig. 3) is higher than the other two. During the subsequent dehiscence after such a maximum volume increase more gametes were liberated than on the previous occasions. While it is possible that some correlation exists between these periodic volume changes and the spring tides, as Lloyd Williams (1905) has shown for the dehiscence of sexual cells of Dictyota, the data at present available for *Ascophyllum* do not permit such a relation to be demonstrated.

The first visible signs of gamete formation on the shore were the orange-coloured sperms developing in the conceptacles of the somewhat translucent male receptacles. Investigation showed that this was followed, after a few days, by the appearance of cleavage walls of the oogonia in the female plants. These visible signs of gamete development normally occurred in late January (1939), but, if the temperature was very low at this time such development was often delayed for about a fortnight as in February 1940 and February 1941.

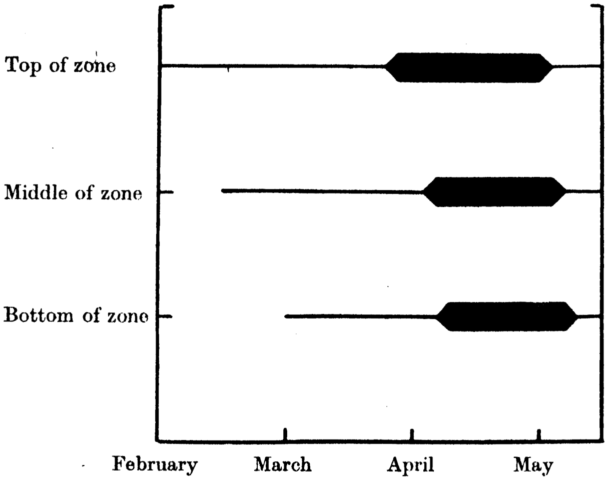

Fig. 5. *Ascophyllum nodosum* Le Jol. Table of dehiscence of male and female plants.

In view of the dioecious nature and the different chemical constitution of the male and female exudates (Heilbron, 1942), it is of interest that maturity of the sperms and eggs should coincide so closely. About one day before dehiscence took place the receptacles underwent a change which rendered them translucent. Such a change was first noticed in the receptacles of the male plants, but was followed in a few days by a similar occurrence in the female plants. Although some dehiscence of a few sperms and eggs took place in February the main wave of dehiscence downshore started in the early days of April, often with the first few days of warm weather (Fig. 5). Dehiscence began in the receptacles near the apices of the plants and extended to the proximal regions in about one or two days. Within seven days of its general initiation in April, this wave of dehiscence spread from the plants at the top of the zone to those at the bottom, the antheridial plants always dehiscing before the oogonial in any particular region. This dehiscence difference in the sexes was borne out by timing dehiscence in the laboratory. When mature male and female plants of the same age and from the same part of the zone were placed under separate bell-jars, the male plants showed a marked dehiscence in a few hours which was not evident in the female plants until later the same day or even the following day. It seems possible that the difference in time of dehiscence from the distal to the proximal receptacles of any one plant, as for the plants from the top to the bottom of the zone, is one caused by changes of humidity. The distal receptacles on a plant, and the plants at the top of the zone respectively, undergo greater changes of humidity than do the proximal receptacles and the plants lower down the zone and are therefore the first to respond. There does not appear to be any rhythm in the discharge of conceptacles in any one receptacle.

The conceptacles of *Ascophyllum*, unlike the unilocular sporangia of *Laminaria*, discharged their contents, under experimental conditions, into fresh or distilled water, though the antheridia thus discharged do not normally liberate their gametes, and both antheridia and oogonia tended to aggregate together in masses and to form flocculent groups. This is due, in part, to the fact that whilst in sea water the discharge is composed mostly of gametes with only a few antheridia and oogonia which soon released their gametes, in fresh water the gametes are not similarly discharged. In this respect *Ascophyllum* and the Fuci differ from the *Laminaria*, which will not discharge their zoospores into fresh water.

By the middle of May dehiscence of gametes from both sexes had stopped, and it was at this time very difficult to find plants in any part of the *Ascophyllum* zone which were dehiscing in more than one isolated receptacle, generally a proximal one, on any one plant. This period was marked by the 'exfoliation' of receptacles caused by the decay of the stalks. These 'exfoliated' receptacles were to be found in pools and gulleys from high to low water, remaining there during June and July. During this time the processes of decay and decomposition, begun on the thalli, continued until no trace of the receptacles could be found anywhere on the shore. This organic deposit in the higher rock-pools was no doubt responsible for the high nitrogen (ammoniacal and albuminoid) values obtained there on analysis of the waters. The early stage of decay of the receptacle stalk was at first more marked in plants at the top of the zone, although it was setting in lower down in May. In almost every plant, young or old, the stalks of the receptacles at the apex of each thallus were at first decayed to a greater degree than those lower down. This was true of both male and female plants. The decay of the stalk was accompanied by a deflation of the receptacle, although quite a number of conceptacles still bore unliberated antheridia and oogonia at this time. The decay started most frequently at the point of attachment of the receptacle stalk to the thallus and then proceeded up the stalks to the receptacles which eventually became soft and gelatinous. The receptacles broke away either at the junction of stalk with thallus or at the junction of stalk with receptacle, in which case the stalk either fell away in one or two days or remained insecurely attached as a shrivelled whitish stalk. In the experiment set up to see whether new receptacle branches would develop if those already formed were removed in January, new outgrowths had appeared by April, and these were free of decay, suggesting that the stimulus causing decay originated in the receptacle and not in the thallus.

From the frequent and periodic shore observations and from more detailed microtomed sections it would appear that this decay was coincident with the appearance of perithecia of *Mycosphaerella ascophylli* in the limiting layers of the receptacle. The appearance of this fungus was first noted by Church (1893). Cotton (1908–9) suggested that the fungus is perennial in the thallus and that it was probable that infection took place at a very early age. There is no evidence of mycelium in the sporeling. Mycelia may be found in the air-bladders of quite healthy plants throughout the year. This phenomenon of decay was common to all plants in Aberystwyth Bay and to plants obtained from other parts of the British Isles at this time of the year. Whether this decay can be attributed directly to *Mycosphaerella* or whether it is in part bacterial can only be ascertained by more extensive research.

Although callus formation occurs on the sieve plates of *Laminaria* no such layer could be discovered in a series of microtomed sections of the receptacles, their stalks, or the adjacent thalli of the *Ascophyllum* plants at this time.

The fact that the exfoliation took place in the days of early summer may be correlated with a change in the length of the photoperiod.

It may be pointed out that, on the Welsh coast and also in other parts of Britain examined at this time, exfoliation of receptacles had normally taken place before initials of new receptacle branches, which will fruit during the following year, were visible to the naked eye. This contrasts with the records for Nova Scotia where Macfarlane (1930–8) showed that new initials are visible whilst the maturing receptacles are still *in situ.*

Ascophyllum *sporelings*

When making observations on the belt transect, which extended from high- to low-water mark, careful search was made for the presence of *Ascophyllum* sporelings. Their absence throughout the greater part of the zone and their occasional occurrence at the top and bottom of the zone and also in the *Fucus spiralis* zone suggests that the conditions of shade, etc., in the *Ascophyllum* zone, except at the extremities, are unsuitable for their development. Wherever the sporelings were found to survive, as in the *Fucus spiralis* zone, they always grew on a rocky substratum where a good deal of detritus was deposited and in which *Cladophora rupestris* and *Enteromorpha compressa* flourished. Frequently the habitat was near the holdfast of *Fucus spiralis,* so that while this *Fucus* gave a good deal of shelter to the sporelings it did not exclude the light completely as did most of the *Ascophyllum* plants in their zone. The appearance of sporelings on sandy substrata, in areas cleared artificially in the *Ascophyllum* zone, suggests that the presence of a suitable substratum and sufficient light were both necessary for the successful germination and development of the sporelings.

Distribution of receptacles on thalli in different parts of the zone

The plants growing in the middle of the *Ascophyllum* zone bore a far greater number of receptacles than plants growing higher or lower on the shore. This is due, in part, to the greater age and, consequently, greater receptacle-bearing capacity of the plants. It must be added that this was true only of uninjured plants up to ten years old. Older plants frequently had no receptacles or had receptacles only on their younger main branches.

The variation in number of receptacles on Ascophyllum nodosum *with the degree of infection by* Polysiphonia fastigiata

The plants in the lower half of the zone, from 0·18 ft. (0·05 m.) above M.S.L. down to 2·16 ft. (0·65 m.) below M.S.L., were, almost without exception, parasitized by *Polysiphonia fastigiata*, the number of infections per frond increasing downshore. It was also observed that the more heavily infected the plants of *Ascophyllum* are by the parasite, the more stunted in appearance they became, and the number of receptacles produced on such plants was very considerably reduced. The average number of receptacles on 100 infected plants was 46 contrasted with an average of 122 receptacles on 100 non-infected plants. The position on the shore, the nature of the substratum, the period of fruiting and other factors were similar for both infected and non-infected plants examined. Further, in most heavily infected plants the receptacles developed only above the region of heaviest infection.

Increase in length of thallus over twelve months

In November 1939 plants of *Ascophyllum nodosum* were chosen at random from the top, middle and the bottom of the zone. These were marked by placing 'chicken-rings' around their bases and by passing cotton through the thalli and knotting the ends. In this way the thalli were divided up into approximately equal lengths, and the exact distance between each cotton strand was recorded at monthly intervals. In order to get comparable readings the plants were measured as soon as they were exposed on the ebb tide. The records indicate that there was a gradual increase in length of a few mm. per month from the setting up of the experiment in November 1939 to May 1940. From May to July the extension was more rapid, frequently showing an increment up to 3 cm. during this period. This rapid increase may be correlated with the shedding of the receptacles in May. These receptacles obviously make a considerable demand on the food resources of the plants during the development and maturation of the reproductive bodies. It is realized, however, that increased assimilation would take place as a result of the increased insolation and the higher temperatures of the summer months. The air-bladders contain gas under appreciable pressure which Damant (1937) maintains is at its maximum in April, the period when the reproductive activity of the plant is at its height. From February to May there was a marked period of reproductive activity, from May to October there followed a period of vegetative growth. In view of the increased pressure in the air-bladders due, according to Damant, to oxygen secreted by the plant, it is probable that during the first nine months of the year there is a good deal of assimilation taking place which could provide a food supply for reproductive activity and vegetative growth. It was ascertained also that increase in length of the *Ascophyllum* thalli was more marked in the apical regions and was only very slight in the proximal and most mature regions of the thalli. That the thalli were affected by light and shade conditions may be seen from a photograph of two plants from the same tide level but which grew under different light conditions (Pl. 12, fig. 3). It will be observed that the shade plant has a greater number of air-bladders, which are closer together than are those on the 'light' or 'sun' plant. The bases of all plants at any one level, except those bearing epiphytic growth, presumably receive approximately equal quantities of light when the plants are covered by the tide because the fronds float vertically in the water. In view of the constancy of lie of the *Ascophyllum* plants and from observations on marked plants during three years, it was assumed that, in general, most of the thalli covered by a number of other thalli after the ebb tide had grown in such conditions and could be termed 'shade thalli', whereas the thalli which lay fully exposed to the sun could be termed 'sun thalli'. The proximal bladders on the 'shade thalli' are much closer together than those on the sun thalli. This is in contradistinction to the higher plants, for where the angiosperms grow in moist and shade conditions they tend to be etiolated and to be longer than plants grown under drier and lighter conditions. Examination of other algae growing in the entrances to caves, in pot holes and under overarching rocks suggests that etiolation is not a phenomenon frequent among the macroscopic marine algae. Frequently only the older portions of the *Ascophyllum* fronds were covered by the thalli of other plants; moreover, the apical regions were exposed to the sun during the ebb tide and therefore developed under better conditions of light. In higher plants higher light intensity tends to depress elongation, but, as a factor in nutrition together with moisture, increased insolation would make for increased length. Measurements of the distances between air-bladders of *Ascophyllum* plants which remained exposed to the atmosphere during the ebb tide and of those plants whose thalli lay in rock pools at low water seemed to indicate that light is a more potent factor than moisture in determining the amount of elongation. It was assumed for the above comparison that the uppermost thalli lying on the rocks were not subjected to greater amounts of insolation than those floating on the surface of the water in rock pools nearby.

Variation in length of plants is affected markedly by such factors as angle of slope of the substratum and by the degree of parasitism by *Polysiphonia fastigiata*. Measurement of fifty plants chosen from both flat and sloping substrata showed the following variation in length:

	Av. length of 50 plants	Range in length
Flat substratum	157 cm.	91–230 cm.
Sloping substratum	96 cm.	63–160 cm.

It is thus evident that *Ascophyllum* plants attained greater length on a flat substratum.

It has been pointed out above that the parasitism of *Polysiphonia fastigiata* affected the number of receptacles occurring on infected plants. In addition, it would appear that this parasite affected the length of the plants. The average length of 100 infected plants was 61·2 cm., whereas that of the same number of non-infected plants from the same zone was 129·0 cm. During the measurements of the increments of growth of marked plants confirmation was secured that a single air-bladder was produced on each branch during the year, November to October. This bladder was produced apically, the growing point emerged beyond it during May continuing the apical growth of the thallus. This observation thus afforded a basis for the estimation of the age of the *Ascophyllum* plants. From the few sporelings of *Ascophyllum* whose development from the very earliest stages had been observed in the field it would appear that no air-bladder was formed in the first year of their existence, but, in the second year, a bladder was formed at about the same time as new bladders developed on older plants. Although no record had been made of the development of new fronds from old haptera, presumably these behave similarly to young sporelings, although it must be borne in mind that these new regenerated fronds develop in the shade of older thalli, evidently deriving the food material necessary for their growth from the mature plant or the persistent base. On the other hand, sporelings failed to develop under these conditions of extreme shade. The sporelings whose development has been observed grew either at the upper extremity of the *Ascophyllum* zone where it forms an open community, or in the *Fucus spiralis* zone. From preliminary observations on *Pelvetia canaliculata* it would appear that a detailed examination of the holdfasts may afford an additional method of estimating the age of plants of *Ascophyllum*, the Fuci and the *Laminaria*.

Knight & Parke (1931) write: 'Longevity is not a well-marked feature of algal life...it is doubtful whether on British coasts the span of life of even these so-called perennials exceeds two or three years.' Rees (1932), while not explicit as to the ages of all the plants at the beginning of his experiment, showed that of the ringed plants which he kept under observation during four years, those of *Ascophyllum nodosum* did not survive longer than two years eight months. During the investigation of a belt transect, examined in detail as part of the shore survey, an estimate of the age of all the plants of *Ascophyllum* in the transect was made by counting the number of air-bladders per frond on at least one frond from each plant, generally the longest arising from each holdfast. Before such a count could be performed successfully reference had to be made to the results of regeneration experiments. These experiments showed that when any portion of the thallus above the basal (proximal) bladder was removed artificially, new branches grew out from the lateral meristems situated nearest to the point of injury. When the thalli were cut below this basal, proximal bladder no new branches were formed, presumably because of the absence of meristematic nodes in these oldest parts of the fronds. In this latter experiment, as in all other cut plants and uninjured plants, regeneration took place from the hapteron.

When the plants were severed artificially at the time of bladder formation just above the newly forming bladder, a new branch grew out from the meristem next below. This new branch developed a bladder, often quite small, soon after the branch had attained a length of about 1 cm. In the following year bladder formation on this newly formed branch took place at the same time as on uninjured thalli. The age of a plant which had been injured at any point above the basal bladder could thus be estimated by counting the number of air-bladders on the parent thallus and continuing the count on the branch formed as a result of the injury. One year must be added to this total, since no air-bladder is formed during the sporeling year.

The ages of the plants examined in the belt transect can, perhaps, be best illustrated by a consideration of plants in different parts of the zone where, apart from variation in length of plants growing on flat or sloping substrata and those with or without the parasitic *Polysiphonia fastigiata*, there is a variation in length and in age probably to be correlated with exposure. At the extremities of the zone the plants probably live under limiting conditions of exposure. Also, in the lower regions of the zone the *Ascophyllum* plants are parasitized, as shown by their stunted nature. This will affect the food supply of these plants as well as their resistance to wave action, the host with the parasite offering a much greater surface to the buffeting of the waves than do the slender uninfected thalli. In the upper and lower limits of the zone the thalli of *Ascophyllum* were approximately equal in length though their ages did not agree so closely. The majority of the plants at the top of the zone were from four to five years old, the remainder there varying in age from six months to nine years. The youngest plants growing at the bottom of the zone were at least four years old and the oldest twelve years, the average being six or seven years. There was a good deal of regeneration from the haptera. The plants in the middle of the zone were interesting because they showed a correlation with the plants at the extremities.

The plants in the upper middle of the zone showed a gradual transition in length and age with the upper extremity and those in the lower middle were occasionally parasitized by *Polysiphonia fastigiata*. The oldest plant recorded in the belt transect was fifteen years old, and this occurred in the middle of the zone. There were a few others in the same locality varying from twelve to fourteen years old; the majority, however, ranged from five to eleven years, eight years being a very common age. The plants which were parasitized in the lower middle part of the zone were much younger, the majority being only four or five years old. This, however, is not to be correlated entirely with the parasite, since the plants were growing on rocks which were slightly higher (up to 0·3 m.) and were free from the worm casts of *Sabellaria alveolata*, so the only available holdfast was a rock crevice. Probably the older plants were more frequently dislodged from this part of the shore as a result of the increased strain on the holdfast caused by the additional bulk of the parasite and to the lack of a really good substratum.

Among the possible reasons for the plants in the middle of the zone (from E.H.L.W.N. to M.S.L.) attaining a greater age is the fact that in this region neighbouring rocks afford an appreciable amount of shelter. Moreover, at no time during the three years during which this part of the shore was under constant observation was any wave seen to break down the channel between these higher rocks. The water rather runs in quietly, and only when the *Ascophyllum* plants are floating vertically do the waves of the incoming tide begin to break, so that none of these plants receive the full force of the breakers but only a long pulling force or drag which this species can easily withstand (Delf, 1932). It must be assumed, too, that the conditions of nutrition, desiccation and the rocky substratum covered by *Lithothamnion* and *Sabellaria* all play their part in providing the life conditions necessary to produce luxuriant vegetation in the middle of the zone, and that such conditions are not found at the extremities, for not only were the plants of greater age in the centre but the plants of any particular age were generally longer than those of a corresponding age at the extremities. Moreover, as mentioned earlier, these plants in the middle of the zone showed a higher percentage of monopodial growth than corresponding samples of plants from the extremities. This monopodial growth, which may or may not be influenced by the conditions of the habitat, would account for the greater length of these plants.

Underflora in the Ascophyllum *zone*

Among the factors which seemed to determine the nature of the underflora were:

(1) Nature of the consociation (whether open or closed).
(2) Screening and covering of substratum by *Ascophyllum* fronds.
(3) Nature of substratum.
(4) Height above or below M.S.L.

Ascophyllum forms a closed consociation except for a few metres at the upper and lower extremities of the zone.

The underflora is best considered in relation to the tide levels ranging from M.H.W.N. down to E.H.L.W.N., and the algae are of especial interest in relation to seasonal changes and recolonization which it is hoped to describe more fully in a subsequent paper. The following lists give characteristic groups of associates:

(*a*) *Top of consociation from* M.H.W.N. *down to* E.L.H.W.N.

Substratum: bare rock with large patches of *Lithothamnion lenormandi* Fosl.

Ulva lactuca L. (whole year, but more abundant in autumn)
Ulothrix flacca Thur.
Cladophora rupestris Kutz. (whole year)
Cladostephus spongiosus Ag. (whole year)
Fucus sporelings (more abundant in summer)
Laminaria sporelings (occasional in winter)
Gelidium corneum Lamour. (whole year)

(*b*) *High rocks just below* E.L.H.W.N.

Substratum: bare rock, sand and sand-tubes of *Sabellaria alveolata* in crevices.

All the algae present under (*a*) above and in addition:

Chaetomorpha tortuosa Kutz.
Sphacelaria cirrhosa C. A. Agardh. (summer)
Corallina officinalis Linn. (whole year)
Polysiphonia nigrescens Grev. (whole year)

(*c*) *From* E.L.H.W.N. *down to* M.S.L.

Substratum: chiefly hard sand-tubes of *Sabellaria* covered with *Lithothamnion Lenormandi*. *Lithothamnion* colonizes the smooth south-west slopes and provides a sufficiently rough and stable substratum, so that *Ascophyllum* and other species in the underflora thrive on areas which would otherwise be bare.

All the algae present under (*a*) above and in addition:

Enteromorpha prolifera J. G. Agardh. var. tubulosa Reinb.
Polysiphonia nigrescens Grev. (whole year)
Ceramium rubrum Ag.
Rhodymenia palmata Grev.

Except for *Polysiphonia nigrescens* the above species appear in spring, flourish throughout the summer and die down in winter.

(*d*) *From* M.S.L. *down to* E.H.L.W.N.

Substratum: sand-tubes of *Sabellaria*.

The underflora here is essentially similar to (*a*) and (*c*) above except that it is present in greater abundance. There are, in addition:

Pilayella littoralis Kjellm.
Corallina officinalis Linn.
Laurentia pinnatifida Lamour.
Lomentaria articulata Lyngb.

The chief seasonal change in this, the lower region of the zone, was the spring increase in the number of species composing the underflora, the number and spread of these species attaining a maximum in summer followed by an autumn and winter decrease in both number and cover of species. Two further outstanding changes were the summer dominance of *Enteromorpha prolifera* and the autumn to winter dominance of *Ulva lactuca*. This interesting succession is particularly evident in the recolonization of the cleared areas.

Where *Sabellaria* was absent, as on the north-east side of the College rocks, the underflora was composed chiefly of *Fucus* sporelings. It would appear that *Sabellaria* is essentially a primary colonizer of the smooth rock surface providing a suitable habitat for many algae especially between M.S.L. and E.H.L.W.N.

Epiphytes

Pilayella littoralis Kjellm. is an abundant epiphyte on plants in the lower part of the *Ascophyllum* zone. It is not here restricted to those apices of the *Ascophyllum* plants which remain in the rock pools as it is in the middle and upper parts of the zone. Nor is it limited to the *Ascophyllum* plants but extends to the substrate and frequently appears as a brown skin stretched over the plants and the substrate left exposed at low water.

The chief differences between the reproduction of *Pilayella* at Aberystwyth and that recorded by Knight (1923) are the absence at Aberystwyth of plurilocular sporangia in spring and the sparsity of both types of sporangia in August and September. Other less frequent epiphytes on *Ascophyllum nodosum*, especially in the bottom of the zone and on plants whose apices lay in rock pools were:

Ulva lactuca Linn.
Fucus vesiculosus Linn.
Fucus serratus Linn.
Fucus sporelings

Endo-parasites in Ascophyllum

(1) *Ectocarpus brevis* Sauv. In February 1940 a *Verrucaria*-like mat occurred towards the proximal regions of old plants growing at the bottom of the zone. Among the vegetative filaments forming the mat both unilocular and plurilocular sporangia were found. The endo-parasite was almost undoubtedly *Ectocarpus brevis*. This may be the first record of the occurrence of unilocular sporangia in this species.

(2) *Acrochaete parasitica* Oltm. This is another endo-parasite found during autumn and winter.

SUMMARY AND CONCLUSIONS

1. Studies in the autecology of *Ascophyllum nodosum* in its wide consociation on the College rocks at Aberystwyth showed that it attained maximum growth and luxuriance under somewhat sheltered conditions. Other nearby rocks, subject to increased exposure, showed much smaller consociations of *Ascophyllum*. Moreover, within the confines of Aberystwyth Bay on these different rocks the zonal positions of *A. nodosum* and *Fucus vesiculosus* were interchanged. Wherever *F. vesiculosus* appeared above the *Ascophyllum* these latter plants were always much shorter.

2. Under suitable environmental conditions, as in the middle of its zone, *Ascophyllum* forms a practically 'closed community', the plants being comparatively long-lived and attaining considerable length. The community thus exhibits a striking stability and continuity not achieved in other consociations on these rocky shores. When this continuity was broken, as was done artificially by clearing certain areas, interesting and surprising recolonization results were obtained.

3. The width of the *Ascophyllum* zone may perhaps be correlated with tidal behaviour, approximating to that area covered by the middle two-hourly period of the flow of the neap tide.

4. The plants in the middle part of the zone attained greater length, possessed larger air-bladders, and produced a greater crop of receptacles than plants at the extremities of the zone. The greater length was accounted for, in part, by the greater average age and by the higher percentage of monopodial growth of the thalli. *Ascophyllum* plants growing on rocks and exposed during the intertidal period at any level on the shore showed more monopodial than dichotomous branching, whilst plants left lying in rock pools at low water showed a slightly higher percentage of dichotomies. Other important factors influencing the length of the plants were the nature of the substratum, whether sloping or flat, and the frequency of the parasitic *Polysiphonia fastigiata*.

5. Growth is apical, the greatest increment occurring during the period from May to July (often about 3 cm. during this period) whilst only a few mm. per month were added during the colder months (November-May).

6. One air-bladder was normally formed near the apex of each branch during each year of growth after the first sporeling year when no air-bladder was formed. Exceptional formation of an additional bladder was induced on the main vegetative branches by injury to the single annual bladder. The number of air-bladders on a thallus from apex to base thus provided a means of estimating the age of the plants. The ages of plants in the broad zone on the College rocks at Aberystwyth varied in the different parts of the zone:

Top: ranging from 6 months to 9 years. Average 4–5 years.
Middle: ranging from 5–15 years. Average 8 years.
Bottom: ranging from 4–12 years. Average 6–7 years.

7. Receptacle branches arise from lateral receptacle pits; at the base of each of these about twelve apical cells are differentiated. Each of these can potentially give rise to either a lateral vegetative shoot or to a receptacle branch. Normally three or four only grew out, but in later seasons others of these meristems functioned to give rise to further receptacle branches. Rarely were any receptacle branches produced beyond the apical bladder and none at the base of the plant. The greater number of receptacles on any plant was therefore produced from the upper middle region of each thallus branch.

8. General dehiscence of the gametes in this country took place about the first days of April, usually coincident with the first few days of warmer weather. Dehiscence was preceded by a translucency of the receptacles and, in any part of the zone, the antheridia discharged slightly in advance of the oogonia. Dehiscence began from receptacles at the apex of each plant and at the top of the zone proceeding to the distal receptacles on any individual plant in about two days and from top to bottom of the wide zone in about a week after initiation.

The writer wishes to acknowledge the kindly help of Professor L. Newton (University College of Wales, Aberystwyth) throughout the course of the ecological work of which this paper forms a part.

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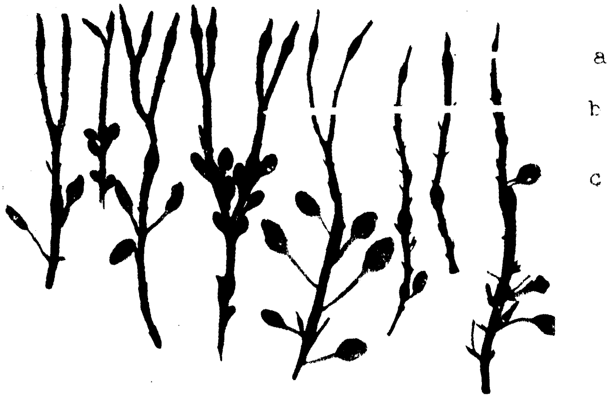

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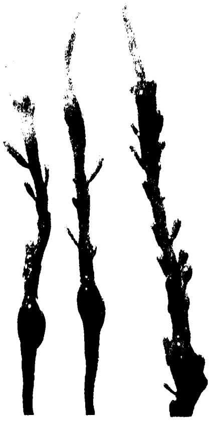

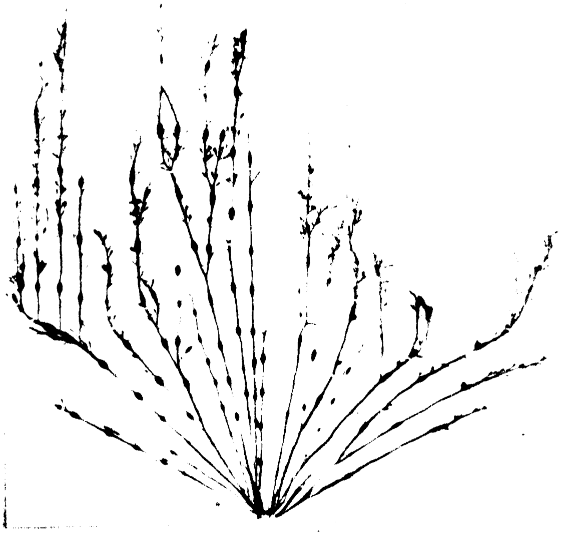

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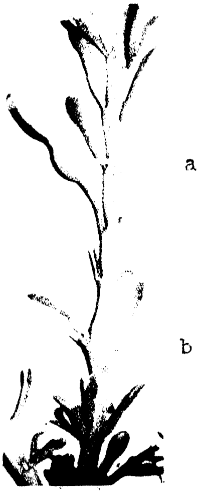

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Fig. 1. *Ascophyllum nodosum* Le Jol. Distal regions of plants. *a*, monopodial branching; *b*, stages in dichotomy; *c*, distal development of receptacle branches.

Fig. 2. *A. nodosum*. Two-year growth with annual air-bladders.

Fig. 3. *A. nodosum*. Shade plant (left) and sun plant (right). The air-bladders are much closer together in the shade plant.

Fig. 4. *A. nodosum*. *a*, Air-bladder on receptacle branch; *b*, nodal air-bladder.

COASTAL PEAT BEDS OF THE BRITISH ISLES AND NORTH SEA

PRESIDENTIAL ADDRESS TO THE BRITISH ECOLOGICAL SOCIETY 1943

By H. GODWIN, *Botany School, Cambridge*

(*With twenty-four Figures in the Text*)

	PAGE
I. INTRODUCTION: STRATIGRAPHY, FORMATION AND ANALYSIS:	
(i) Plant content and conditions of formation	199
(ii) Coastal peats as evidence of former sea-level	204
Dating of coastal peats by pollen analysis	205
(iii) Eustatic and isostatic factors in land- and sea-level change	208
II. BRITISH COASTAL PEATS:	
(i) South coast	211
(ii) West coast	216
(iii) Scotland	226
(iv) Ireland	229
(v) North Sea and east coast	234
CONCLUSIONS	245
REFERENCES	246

I. INTRODUCTION: STRATIGRAPHY, FORMATION AND ANALYSIS

At places all round the long coastline of Britain, and along part of the western shore of the Continent there are found from time to time peat deposits clearly once formed in fresh water, but now either within reach of the tides or submerged permanently. Sometimes these beds are particularly striking in that they support the stumps of woodland trees, and to these submerged forests the term 'Noah's woods' has been applied. So apparent indeed is the evidence they convey of change in sea- and land-level, that they have long been adduced in proof of such alterations. Geologists have rightly insisted (e.g. Penhallow, 1907; Johnston, 1913) that where such beds are but little submerged they need not necessarily have come to their present situation as a result of a relative shift in level of land and sea, but rather that other local coastal physiographic factors have produced the effects now seen. There can, at the same time, be very little doubt that in a great majority of instances the submerged peats truly reflect marine transgression.

On this account interest has long concerned itself with the evidence of dating which these beds afford. The content of archaeological material is disappointingly small, and what there was, for long was referred to the 'Neolithic' period in the very wide original sense of that term, which covered all that long period we now call the Mesolithic, the Neolithic *sensu stricto*, and perhaps also sometimes the Bronze Age, or even the Iron Age. Usage became fashionable of the term 'The neolithic submerged forest period', but as we shall show, the time has now come to abandon finally this phrase and its underlying concepts.

(i) *Plant content and conditions of formation*

The content of identifiable plant material, despite much decay during formation, and perhaps also during later exposure on the beach, is often fairly high, and it is frequently possible to recognize the vegetative parts of the plants which made up the peat, and also by means of seeds and fruits to get some notion of the flora present when a bed was formed. Thus Clement Reid, from analysis of the 'moorlog' on the floor of the North Sea (Reid, 1913), concluded that most of the species present were typical of fresh-water fen and represented a more northern climate than that of the same latitudes to-day. Short of this, however, the plant identifications were not very helpful, for all were of species still within our own flora: the deposit was not old enough to include plants now extinct here, and except in rare interglacial beds we cannot expect to find such in our coastal peats. Identification of fruits and seeds may of course still be most profitably pursued, not only to establish climatic and edaphic conditions during formation of the bed, but also to trace by correlations with all dating indices which may be available, the actual occurrences of our native plants in the different stages of our prehistory. This sort of interest attaches to recent seed identifications from a late Bronze Age coastal site in Minnis Bay, north Kent, where *Coriandrum sativum*, *Spergula sativa* and *Lythrum hyssopifolia*, along with other species, were recently identified (Conolly, 1941).

In the course of identifying plant remains in the peat, wood, leaves, bud scales, rhizomes, seeds and fruits may be made use of, and, among other structures, pollen grains. The sum total of this information often permits a close estimate of the nature of the peat deposit and of the type of plant community by which it was produced. Indeed, in many instances, a sequence of coastal deposits may be seen to reflect a complete history of vegetational succession such as is now indicated by zonation of living vegetation. A very common sequence is the kind brought to light by Swinnerton's thorough investigations on the Lincolnshire coast (Swinnerton, 1931) (Fig. 1).

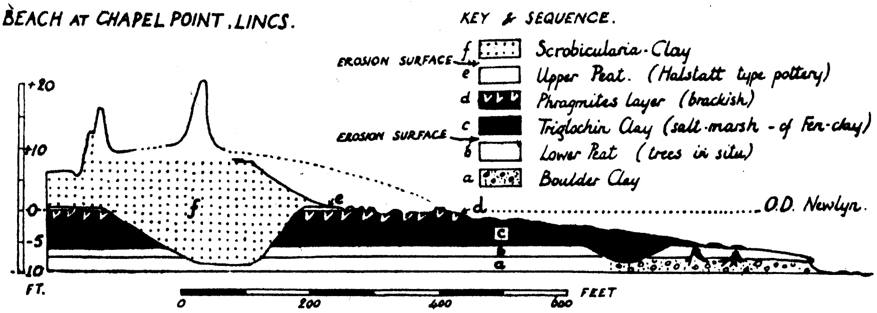
BEACH AT CHAPEL POINT, LINCS.
KEY & SEQUENCE.
EROSION SURFACE
f Scrobicularia-Clay
e Upper Peat. (Halstatt type pottery)
d Phragmites layer (brackish)
EROSION SURFACE
c Triglochin Clay (salt-marsh - of Fen-clay)
b Lower Peat (trees in situ)
a Boulder Clay
+20
+10
0
-5
-10
FT.
f
e
d
c
b
a
O.D. Newlyn.
0
200
400
600
FEET

Fig. 1. Diagrammatic profile of shore deposits at Chapel Point, Lincolnshire, after Swinnerton (1931), showing two coastal peat beds, the lower a forest bed on boulder clay and the upper a fen-wood peat. (Reproduced from *Philos. Trans.*)

Here there is a basal peat bed with oak-stools, rooted some in the underlying boulder clay, and some in the peat above this: overlying this is some 6 ft. of clay with abundant though decayed plant remains in its blue-grey upper and lower layers. The following plants were recognized: *Triglochin maritimum* (at first thought to be *Posidonia*), *Juncus maritimus*, *Statice*, and *Armeria*. The central purple clays contain only black vertical streaks suggestive of the roots of *Salicornia*, and above them come in sequence layers with abundant *Juncus maritimus*, then *Juncus* with abundant *Triglochin*. Next these two plants disappear and the rootstocks of *Statice* and *Armeria* replace them, and still higher *Phragmites* predominates, the beds with this plant passing continuously into the overlying pure *Phragmites* peat. Locally the *Phragmites* peat passes upwards into a peat containing small wood of *Salix* and *Taxus*, together with abundant tree leaves. It is quite apparent that this series expresses a complete cycle of saltmarsh succession from though certainly they will be more prevalently formed at times when climatic conditions favoured extension or renewal of bog growth.

From Lochar Moss Erdtman reports the extraordinarily deep profile below:

A (i) 0–260 cm., much decayed *Sphagnum* peat.
(ii) 260–310 cm., slightly decayed *Sphagnum* peat.
(iii) 310–460 cm., much decayed *Sphagnum* peat.
B 460–760 cm., peat with *Menyanthes*, *Cladium* and *Thelypteris*.
C 760–798 cm., clayey nekron mud.
D 798–818 + cm., rhizome-bearing grey clay.

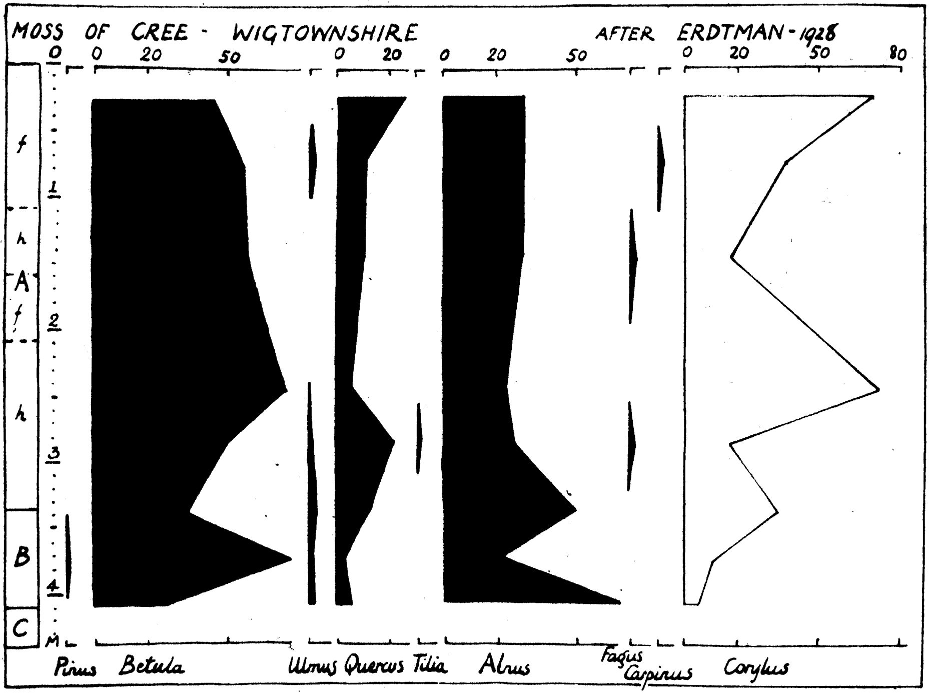

Fig. 17. Pollen diagram from the Moss of Cree, Wigtownshire (after Erdtman). *A* = raised-bog peat, *B* = wood peat, *C* = silty clay: *f* = fresh, *h* = humified peat. This peat bog lies on the 25 ft. raised beach.

A sample at 790 cm. yielded *Be* 45%, *Pi* 2%, *Ul* 3%, *Q* 29%, *Al* 21%, *Co* 15%. Although Erdtman comments that in spite of the great depth the basal peat is of the same age as in the Moss of Cree, 'chiefly sub-Boreal and sub-Atlantic', it seems to us that here also a greater age is probable, though evidently not so great as to predate the time of the alder's extension at the expense of pine and birch.

If we set aside a natural tendency to discover that the carse clays and 25 ft. beach correspond with the Scandinavian *Littorina* beaches, neither of the two Scottish manifestations can be said to have been at all closely dated by the pollen analyses, nor will this be achieved until specific research is undertaken for this purpose. Such research would, however, be very well worth while.

Meanwhile it remains to point to one further result of outstanding interest. Dr Blackburn (1940) reports briefly that the island of Soay, just off the south-west corner of Skye, provides some remarkable evidence of the maximum marine transgression. The two parts of the island are separated by a low peaty isthmus, and close beside, but at a higher level, lies a small lake containing at the bottom 9 in. (23 cm.) of fresh *Sphagnum* peat, then 1 ft. 6 in. (46 cm.) of gritty clay, a grey-brown mud of similar thickness, and then a fibrous lake deposit changing gradually at the top to a *Sphagnum* peat. The total depth was 10·5 ft. (3·2 m.). It turned out that the grey-brown mud contained abundant salt-water diatoms, an indication in all probability of the phase of marine transgression which built the section of 25 ft. raised beach present close at hand on the island. The lake mud over this deposit contains desmids, which are safe indicators of the return of fresh-water conditions. Dr Blackburn has prepared a pollen series through the whole of this sequence of deposits, and from this (Fig. 18), which she now kindly allows me to publish for the first time, it appears that the basal *Sphagnum* peat is Boreal in age (zone VI), whilst the marine clay comes in very near to the transition between zones VI and VII.* The site is fortunately placed, for it must represent the *maximum* extent of the marine transgression, which transgression would thus appear, at Skye, to have been practically completed before zone VII. We cannot, unfortunately, learn from the diagram when it was that fresh-water conditions replaced marine, for too little is yet known of the detailed drift of Scottish forest history in the latter part of the post-glacial period.

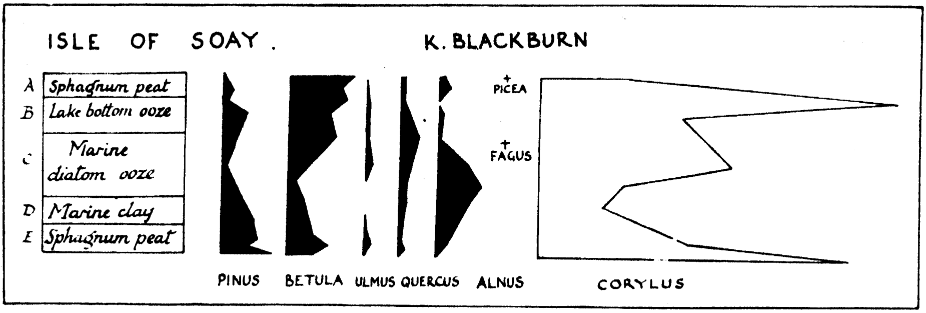

Fig. 18. Pollen diagram from data given by Dr K. B. Blackburn from the Isle of Soay, near Skye, on the isthmus in the centre of the island. Deposits C and D are presumed to represent the 25 ft. beach marine transgression.

A little further archaeological evidence exists in the Azilian shell-mounds on the 25 ft. beach at Oronsay, and Azilian remains from a cave at beach level at Oban. Unfortunately this Mesolithic culture cannot be closely dated in Scotland, particularly since it appears to lie on the very fringe of the Azilian culture area and at the same time reflects an indigenous continuation of Palaeolithic cultures (Clark, 1932).

(iv) *Ireland*

There is much submerged peat round the coasts of Ireland: it has been reported equally from the Atlantic, Irish Sea and English Channel coasts, but pollen-analytic examination

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* Such a determination rests a good deal on the assumption that the extension of *Alnus* was here contemporaneous with its English extension. If delayed, as in Ireland, it is possible that the reference should be to a post-Boreal zone.

Kurischer Haf, represented in all its stages by living communities (Steffen, 1931). Succession of this kind through fen wood and birch-pine 'Übergangsmoor' to raised bog cannot, I think, now be seen anywhere in living communities round the British Isles, but our coastal peat beds give clear evidence that it formerly occurred. Thus at Ynyslas on the coast of Cardiganshire the analyses made by Mrs Campbell James of the submerged peat on the shore were shown to indicate in all probability the sequence brackish water clay → fen → fen alder-woods → birch-wood → pine-wood → *Sphagnum* peat (Godwin & Newton, 1938). This probability has been strengthened by a line of borings subsequently made from the shore peat inland to the great raised bog, Cors Fochno, which lies behind the coastal ridge of dune and shingle. This profile clearly indicates that the whole bog is of similar structure and origin, so that the coastal submerged peat is only the lower part of the bog now carried below sea-level and suffering erosion as the shingle spit moves inland across its margin. The big pine stumps of the 'Übergangsmoor' stage are found not only on the coast, but below the old *Sphagnum-Calluna* peat where the artificial channel of the Leri now cuts through the bog (see p. 223).

Of the profiles so well described by Munn-Rankin in *Types of British Vegetation* (Rankin, 1911) there can be little doubt that those of the Lonsdale Estuarine moors indicate precisely the same complete vegetational succession to a raised-bog climax.

It can well be imagined that for such a vegetational succession from brackish water to manifest itself fully, either in a zonation of living vegetation or in the fossil form we have been discussing, a stationary or rising coastline is essential. It is possibly on account of recent submergence that we do not find the communities of this succession round British coasts to-day, but must turn for them to the southern Baltic. Only a general tendency for the fen woods of the East Anglian Broads to develop towards ombrogenous communities suggests the operation of appropriate developmental factors, which are, however, not allowed full play by the influence of a subsiding coastline and by the human interference with drainage (Godwin & Turner, 1933).

Before concluding our consideration of the immediate interpretation of the plant content of coastal peats, a few subsidiary observations may be made. In the first place, by no means all the woodlands represented by 'submerged forests' were necessarily fen woods. In many instances the trees are deeply rooted into the mineral soil of boulder clay or more ancient deposits, and evidently grew thus as upland forest. The death and preservation of the trees alike were caused by a rising water-level which caused peat to form over the ground, and to bury the stubs and fallen trunks before they could decay. Such waterlogging might follow from backing up of fresh water during progress of a marine transgression, but other climatic and topographic causes can readily produce the same effects, and in particular an expansion of area covered by a raised bog results in the very familiar bog profiles with the bottom deposits consisting of wood *in situ* on mineral soil. The trees of the lower peat bed at Ingoldmells on the Lincolnshire coast were thus shown by Swinnerton to be rooted in the boulder clay (see Fig. 1), and this is true of the lower layers of 'the buried forests' of the East Anglian Fenland margin.

A further point of interest is the occurrence in coastal deposits of layers of so-called 'marine' peat (Chapman, 1941). The limits of applicability of the term 'peat' have never been closely set, and under brackish or littoral conditions many kinds of deposit may be laid down with high organic content, and at the same time a great deal of silt or clay. In this category we have already mentioned the brackish water 'Darg' or *Phragmites* clay, but in addition Chr. Brockmann has reported fen-wood peat containing salt-water diatoms. Scandinavian workers speak of 'marine Gyttja'; from tropical waters mangrove-rootlet peat is described (Chapman, 1940*a*), and from the New England and from Irish saltmarshes also a fibrous rootlet peat of high silt content has been mentioned (Chapman, 1940*b*, 1941). In addition, lines of drift with more or less algal debris may become buried and converted to a peaty mass, and there can be little doubt that many such types remain to be reported and correctly referred to their conditions of origin.

(ii) *Coastal peats as evidence of former sea-level*

Although it is quite apparent that a forest peat grounded on hard rock and now deep below mean sea-level must indicate a marine transgression, the exact extent of the relative shift of land- and sea-level indicated by coastal peats does, in general, demand some careful consideration. In the first place, of course, aquatic deposits, both organic and inorganic, commonly have a high initial water content, and when accumulating in thickness they suffer considerable compression. If this is neglected, it may appear that a given peat layer was formed when the land stood some feet higher in relation to the sea than need necessarily have been the case. Nevertheless, since the rate and magnitude of this compression is usually unknown, it has not been possible to allow for its effects in the discussion which follows of relative change of land- and sea-level round the British coasts. When we deal with recognizable saltmarsh deposits we often have a close guide to former sea-level, for as Chapman has shown in his studies on the coast of Norfolk (Chapman, 1938), the different stages of the halosere lie at well-defined heights between mean sea-level and the high-water mark of spring tides, and we may indeed place the transition from saltmarsh to *Phragmites* marsh very close to this latter level. Nevertheless, it must be remembered that even calculation from this involves the assumption that the local tidal range has not been altered since the saltmarsh deposits were formed. This is an assumption not always easy to make on coasts where the growth or removal of spits and banks may easily alter the tidal range by some feet.

Where a fen wood can be shown to have succeeded a saltmarsh in the coastal series, we are, I think, justified in supposing that the trees grew at a level at least half the full tidal range above mean sea-level, but such an assumption by no means holds for every fresh-water peat or fen-wood peat. Thus, for instance, at the present day in the Norfolk Broads fen peat is forming beside shallow lakes, the water in which is no more than 1 or 2 ft. above mean sea-level, although these same broads are in direct river connexion with the sea. The explanation lies, of course, in the fact that the tidal wave passing up the estuary gradually diminishes its amplitude and eventually disappears, so that just upstream of this point the slow river will be little above mean sea-level. The reality of these relationships in level, which were clearly recognized by Reid in 1913, was strikingly demonstrated in the disastrous flooding of the north-eastern Broads in February 1938. This part of the Broads, though a long way from the sea by way of the Thurne and Bure to Yarmouth, was very close indeed to the fringe of coastal shingle and dune, and under conditions of exceptionally high spring tides the sea broke through the coastal defences and flooded Horsey Mere and its surroundings to a depth of many feet. Only repair of the banks and sustained pumping got rid of the sea water, and had human interference not prevailed the fresh-water fen peats growing round the Broads in 1937 might already in 1943 be exposed as 'submerged peats' upon the Norfolk shore well within tidal range, and all this with no necessary change in the relation of land- and sea-level. It will therefore be apparent that in estimating the former position of sea-level by the use of peats now submerged, it will be an advantage to know, where possible, in what relation to the coast and rivers the peat was laid down.

From all we have hitherto said it should be apparent that the most valuable indices to the former land- and sea-level movements will be found not in isolated samples from scattered exposures of submerged peat, but from long vertical series of coastal deposits where the change of conditions with time is registered in a deep sequence of deposits. The optimal conditions are perhaps met by systematic borings and exposures made in quiet, deep estuaries where there has been a long interplay between the formation of marine, brackish water, and fresh-water deposits. Here we may find the landwards extension of silts and clays during phases of marine transgression and the seawards formation of peats during marine retrogression. Always on the seaward side silts and clays preponderate, and when these taper away into the landward peat deposits we shall find the record of the maxima of marine transgression. Because of erosion we are less likely to be able to recognize the exact period of farthest marine retrogression, but its approximate period will perhaps be recognizable in the thinning out alteration of the peat layers towards the sea. In the discussion which follows we shall always find our best evidence in the deep filled-in estuaries, such as the Fenland, the Somerset Levels, and the bays of the submerged lowland coasts of Holland and Germany. Figs. 12, 15 and 22 will show with what similarity of pattern such estuarine deposits are laid down: the nature of this pattern has been discussed elsewhere (Godwin, 1938).

Dating of coastal peats by pollen analysis

The greatest difficulty in investigating changes of Quaternary land- and sea-level is that of finding a suitable geochronology or time scale by means of which they can be set into correct relationship with one another and with other geological events and criteria of the same period. It is the particular value of pollen analysis that it promises at least a partial solution to this difficulty. The method is now too well known to need full description, but we may recall that it is based upon the following circumstances:

(1) The greater part of our natural vegetation is and has long been forest, (2) the woodland trees are wind-pollinated plants and produce pollen in vast quantities, (3) this pollen is incorporated in growing deposits, and when these are waterlogged, the pollen-grain membranes are preserved from decay, (4) a large proportion of the grains have morphological characteristics of size, shape, surface markings, pore number and shape, etc., which allow identification of the tree genera, (5) methods have been worked out by which the humus, carbohydrate and lignin detritus of peats can be removed without destroying the pollen membranes, and similarly the carbonates, silica, and silicates of fine mineral sediments may be removed, or their obscuring effect diminished.

By analysis of the tree-pollen grains recovered from a vertical series of samples through a deposit, the history of woodland growth in that district may be reconstructed right through the period of formation of the deposit. Furthermore, by comparing pollen diagrams thus produced, over a stretch of country, or even of a continent, we can trace with complete certainty the northwards movements of successive forest belts in the post-glacial period of increasing warmth, to high latitudes, and finally a small reversion to those of to-day. As forest history becomes known in any region it naturally becomes linked with archaeological horizons, indications of climate, and indications of important geological changes. In Scandinavia where pollen analysis, like other techniques of Quaternary geology, is long established and highly developed, such correlations are now detailed and elaborate, but in this country we are only in process of establishing the outline of forest history, and making the first outlines of a correlation scheme.

We approach the problems of regional comparison of pollen diagrams by devising for them a zonation system, to illustrate which we may give the characteristics of the zones worked out for the East Anglian Fenland (see Fig. 23). We assume that deposits corresponding to the Upper and Lower Dryas clays and the intervening Allerod layers will be recovered here as in Ireland and Denmark and therefore leave (following the scheme of Jessen) zones I, II, and III to represent them, and begin our zonation with zone IV. This can be considered the opening of the 'post-glacial' period after the 'late-glacial'.

IV. *Birch-pine zone.* This is a zone of dominance of *Betula* pollen, with *Pinus* as the only other important tree. Smaller amounts of *Salix* pollen are present, and in the south and east of Britain small quantities of the warmth-loving trees; small amounts of *Corylus* also occur in some sites, but the ratio of non-tree pollen to tree pollen is so high as to suggest an open landscape, over which these warmth-indicating pollens may have been carried considerable distances.

V. *Pine zone.* This zone in East Anglia seems to show general extension of forest, and in it there is a widespread replacement of *Betula* by *Pinus* as the dominant tree pollen. *Corylus* begins to extend very rapidly, and here and there small amounts of warmth-loving trees are represented.

VI. *Pine-hazel zone.* Zone VI is clearly divisible into three subzones, *a*, *b* and *c*. In subzone VI*a*, *Ulmus* extends swiftly, and *Quercus* though present is less important. The dominant pollen remains *Pinus* in the south-east of England and locally elsewhere, and *Corylus* reaches extremely high values.

Subzone VI*b* differs from the preceding simply in that *Quercus* pollen equals or exceeds that of *Ulmus*: *Corylus* remains exceedingly abundant.

In subzone VI*c* the East Anglian diagrams show the first tendency of *Tilia* and *Alnus* to extend, and *Corylus* is generally much lower than in VI*b* or VI*a*. *Pinus* sometimes shows retrogression before extending mixed oak forest and *Alnus*, but prevalent dry conditions seem often to permit its local and temporary extension.

Zone VI must correspond in time with most of the Boreal climatic period of Blytt and Sernander.

Above zone VI alder and trees of the mixed-oak forest predominate in the pollen diagrams of the south and east of Britain, and further zoning must be rather tentative. We may, however, distinguish zones VII and VIII, with a transition zone VII–VIII between them.

VII. *Alder-oak-elm-lime zone.* The beginning of this zone is indicated by the sudden replacement of *Pinus* by *Alnus* as the most abundant tree pollen. In some places where *Betula* has been maintained in previous zones it may be this tree that recedes before the *Alnus*. *Tilia* expands considerably, and its pollen in East Anglia reaches consistently about 5–10% of the total tree pollen. *Quercus* maintains the values of the previous period or may show some increase. *Ulmus* shows no decrease to begin with, but a decline half-way through zone VII seems to be widespread, especially in the west, and can be used as an index for a tentative subdivision of zone VII into subzones *a* and *b*. Although the *Corylus* pollen curve is so very variable it seems generally true that it is low in subzone *a* and rises considerably in *b*. Small amounts of *Fagus* pollen occur sporadically at different sites in this zone, but have no diagnostic value for it.

VIII. *Alder-oak-elm-birch* (*beech*) *zone*. As mentioned earlier there may be distinguished between zones VII and VIII a transition zone VII–VIII, and this has been recognized in the Fenland and Shropshire studies. There is not yet, however, evidence enough to warrant its employment in a general consideration of England and Wales as a whole, and it will suffice to say that in it the pollen curves change from the proportions of the earlier zone VII to those of the later zone VIII.

Zone VIII is characterized by three principal features: the *Betula* curve maintains higher values than in the earlier zone, the *Tilia* curve either ceases or becomes discontinuous, and the *Fagus* (and to a less extent *Carpinus*) pollen is present in much greater amount than previously, in many sites continuously present although at low values.

In a recent paper (Godwin, 1940*c*) we have attempted the exercise of applying this system of zones to the whole of England and Wales, and although the number of sites from which we can use results is rather small, several points of importance have emerged.

It is apparent that forest history pursued a parallel but not identical course over all parts of England and Wales. Throughout the post-glacial period the warmth-loving trees have always been present in greater amount in the south and east, whilst birch in particular has remained much more abundant in the north and west. The hazel has shown itself an Atlantic species throughout. It is interesting to find that the division of the country into a northern and western division on the one hand and a southern and eastern division on the other, has not only persisted through so long a period, but has been independently recognized at the present day by Prof. Tansley (1939) in his analysis of the country into climatic-vegetational regions.

It is also interesting to note that certain sites influenced by local soil or topographic circumstances show throughout the long post-glacial period persistent differences from other neighbouring sites. This is perhaps no more than ought to be expected from our present experience of vegetational distribution.

In Scotland insufficient work has been done to permit any adequate extension of the zoning to that country, and though more has been published for Ireland we still await publication of the great mass of competent analyses made by Knud Jessen and his colleagues, and already co-ordinated by him in an independent zonation. Nevertheless, for our present purposes of comparing the age of coastal peats we shall have no alternative but to apply so far as possible the English and Welsh zonation to all the regions considered, bearing in mind the qualifications necessary in doing this.

For the correlations which have so far been made in England and Wales between the zonation described and archaeological cultures, climatic indices, the facts of former distribution of plants and animals, etc., it must suffice to refer to publications (Godwin, 1940*c*, 1941*b*).

It would at first sight appear that the submerged peats were entirely suitable to pollen investigation, but they suffer certain grave disadvantages: (1) they often contain much clay and silt of primary or secondary origin which obscures the pollen and makes counting very difficult; (2) they have often suffered secondary decay which has affected their pollen content; (3) as we have seen, they often reflect such tremendous local influences (especially the submerged forests) that the general forest composition of the country is hardly to be recognized; and (4) they occur so sporadically and represent such a short time-duration that it is hard to fit them exactly into either the local geological sequence, or the detailed scheme of forest history for the neighbourhood. Nevertheless, even from pollen analysis of quite isolated submerged peats much can be learned.

One ought also to mention a curious difficulty met with rather consistently in the analysis of series which cross alternately tidal clays and peat beds. Under such conditions, that part of the pollen diagram representing the clays will show an enormous preponderance of *Pinus* pollen, in complete and abrupt difference from the pollen composition representing the peats. This feature is very well shown in the diagram (Fig. 3) by Brinkmann from the north-west German marshes, and indeed in all similar diagrams from this region, from Holland and equally from many sites in the English Fenland. There can be no doubt, since the phenomenon is so widespread and characterizes clays of different ages, that it does not correspond to any real increase in the proportions of *Pinus* in the upland woods, and must not be so interpreted. It clearly is an over-representation of the tree directly due to the conditions of deposition, and there has been speculation from all the authors who have met with the phenomenon as to its cause. Brinkmann (1934) gives a very full discussion of the problem. He rejects the notion that it can be due to differential pollen destruction, and gives some evidence pointing to distant transport as the primary cause. Through the great destruction of fen woods by the marine transgression, the local tree pollen of *Alnus*, *Betula* and *Quercus* is greatly diminished and consequently the distant pollen rain comes to play a far greater role in the pollen spectra of the clays. This distant flying pollen contains a big proportion of *Pinus* pollen either because of its greater capacity for flight, or because the countryside has more pine forest than had the submerged lowlands. Although Brinkmann's explanation is fairly convincing, it must be remembered that pine pollen does not fly farther than the wingless but smaller pollen of other trees, and in addition we know that in the Cambridgeshire Fens the pine was not a preponderant tree in the upland forests during formation of the fen clay. In the Fens indeed marginal pine-woods growing on the peat surface might well have been the source of the pollen in the estuarine clays, although in Holland and north-west Germany this kind of explanation is not advanced. There remains a possibility that pine pollen comes to preponderate in clays by some property of floatation in sea water lacking to the other tree pollens, but there is no evidence of this. It might be supposed also that in course of transgression the erosion of older peats might in some instances lead to an incorporation of secondary pollen, but were this a general explanation excess of *Betula* or other pollen would often replace that of *Pinus*.

(iii) *Eustatic and isostatic factors in land- and sea-level change*

It is widely known to-day that a very close relation exists between the accumulation and disappearance of the ice-sheets on the one hand, and the relative height of land- and sea-level on the other. In the first place the locking-up of vast quantities of water as ice will cause a reduction in sea-level during glacial periods themselves, and the liberation of this water in the warm interglacial climate will cause a corresponding restoration in ocean height. Thus, broadly speaking, the glacial periods will be times of low sea-level, and the interglacials of high level. These changes, it must be noted, affect the ocean level the world over, and are on this account termed 'eustatic'. Many attempts have been made to estimate the rise in sea-level caused by the melting of the Quaternary ice-sheets. Penck, assuming an average ice thickness of 1000 m., arrived at a figure of 66·5 m. (210 ft.). Anteus (1928) gave a figure of 272 ft. Ramsay (1930) gave a revised figure for *maximum* eustatic rise at 183 m. (*c.* 560 ft.). It will, of course, be apparent that eustatic alterations of ocean-level may occur at times other than full glacial periods and perhaps for causes other than changes in glaciation. Thus Daly (1925), who is generally known for his views on glacial control of the growth of coral reefs, considers that in addition to the big post-glacial rise, there is evidence for a more recent eustatic fall in sea-level of 6 m. taking place about 3000 B.C. In so far as eustatic changes in sea-level can be recognized with certainty they will, because of their ubiquity, afford a most valuable means of transferring sequences and chronologies from one part of the world to another, and it is because of this that the aid given to the recognition of eustatic sea-level changes by pollen analysis is of such importance. Jamieson in 1865 suggested the other chief mechanism by which the ice-sheets affected sea-level. This he conceived to be due to a depression of the flexible earth's crust beneath those areas where the ice-load was greatest, so that they suffered some submergence during the ice-age, only to re-emerge on removal of the load by melting of the ice. The fact that raised beaches were found in all the centres of dispersion of the Quaternary ice, and the evidence that these were warped so that they now lie highest where the ice was thickest, most strikingly agree with this theory of 'isostasy' or 'isostatic land movement', and indeed this theory is now generally accepted. These isostatic movements naturally differ from the eustatic in that they affect every area to an extent dependent on its position relative to the crustal ice-load, so that they produce phenomena more difficult to use as chronological indices. The magnitudes of isostatic effects can be seen from the isobase maps of Scandinavia, from which it is clear that some regions now stand over 225 m. above present sea-level, and therefore, adding the eustatic rise of say 70 m., they are at least 295 m. higher than during the glaciation itself. It must be recognized that the isostatic changes in level differ in their time relations from the eustatic, for whereas the latter are an immediate result of the ice melting, the isostatic changes follow only after very considerable delay. Thus, although the eustatic rise was effectively completed many millennia ago, a large part of the isostatic rise of Fennoscandia has taken place since that time, and is indeed still going on. Moreover, the complexity of the isostatic changes is added to by the fact that in all probability the recovery of the deeply depressed regions is accompanied by a subcrustal magma flow which causes in the peripheral regions a zone of temporary depression. To this we may add the possibility that the stresses of these considerable warping movements may cause faulting, which will produce local discontinuities in the traces of land- and sea-level effects.

We shall naturally find that both eustatic and isostatic effects are operating together during a large part of the post-glacial period, a concept developed and expressed by Wright (1914) as the Isokinetic Theory, and now very generally accepted. From what we have already written it will be apparent that to begin with as the ice melted, eustatic effects would preponderate in the glaciated regions, and express themselves as marine transgressions. Later, in some regions at least, the growing isostatic recovery might for a longer or shorter time keep pace with the eustatic rise, so that unchanged relative land- and sea-level would prevail. Finally, with the dying away of the main eustatic rise, isostatic recovery would express itself as marine retrogression. We shall note that the maximum submergence, marking the balance between the two opposing movements, will be earliest in peripheral regions where isostatic recovery is slow, and latest in the

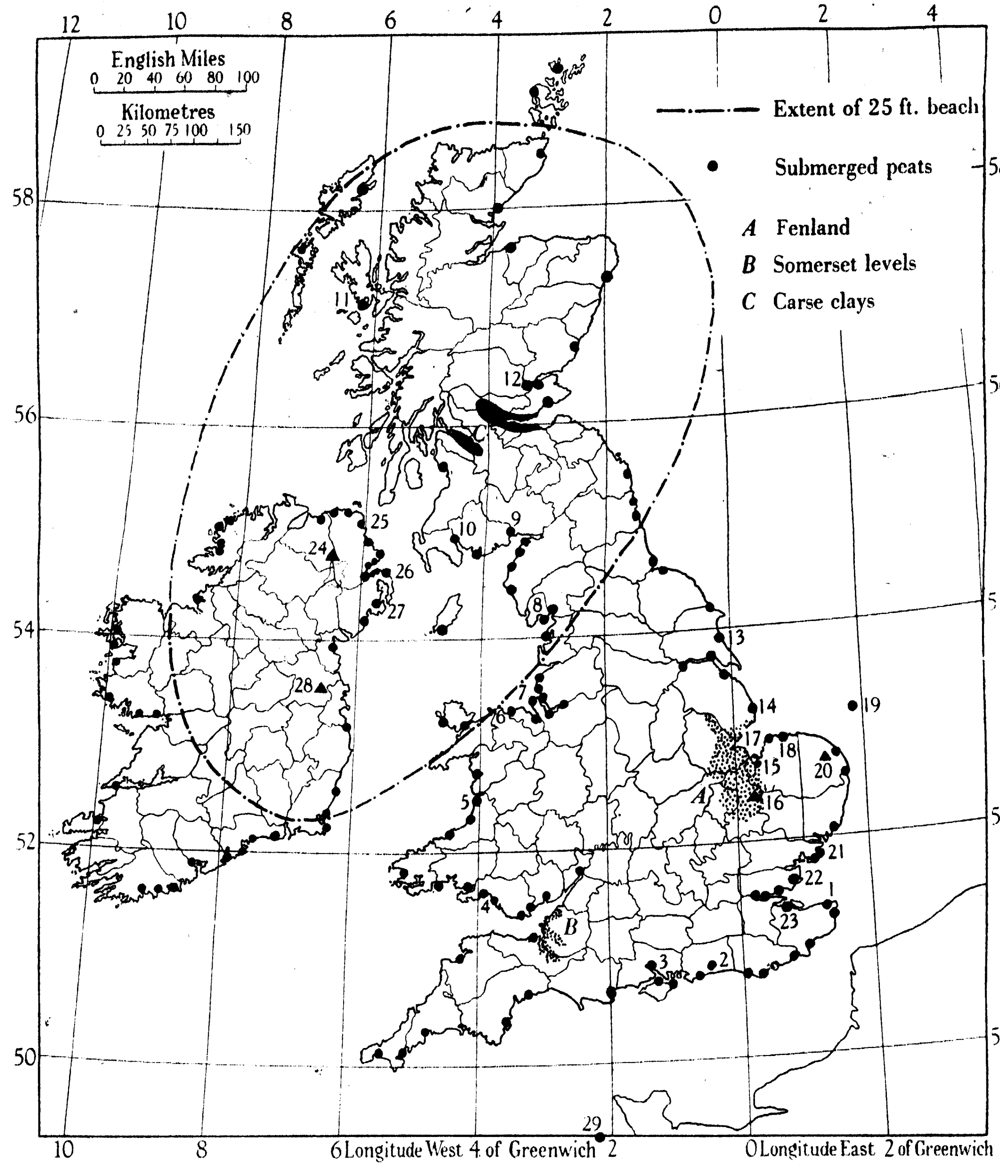

Fig. 4. The map shows the position of submerged peats round the shores of Britain as disclosed by a preliminary survey of the literature. Sites specially referred to in the text are numbered as follows:

(1) Minnis Bay.
(2) Amberley Wild Brooks.
(3) Southampton.
(4) Swansea.
(5) Borth and Ynyslas.
(6) Rhyl.
(7) Leasowe.
(8) Lonsdale Mosses.
(9) Lochar Moss.
(10) Moss of Cree.
(11) Isle of Soay.
(12) Forgandenny.
(13) Skipsea.
(14) Ingoldmells.
(15) St German's.
(16) Old Decoy.
(17) Hunstanton.
(18) Brancaster.
(19) Leman and Ower.
(20) Barton Broad.
(21) Clacton and Walton.
(22) Hullbridge-on-Crouch.
(23) Lower Halstow.
(24) Newferry.
(25) Cushendun.
(26) Island Magee.
(27) Belfast Lough.
(28) Dunshaughlin.
(29) St Helier, Jersey.

(Distribution of carse clays after Jamieson (1865), and of 25 ft. beach after Wright (1937).)

central parts of glaciated regions where isostatic recovery is most rapid. This does indeed appear to be the case in southern Scandinavia.

It is against this complex background of primary causes that we have to consider the problems of dating the submerged forests of western Europe, and there are very clear indications that in the British Isles themselves both eustatic and isostatic effects have to be reckoned with. The peat of the North Sea basin, and the deep Flandrian deposits of the English Channel almost certainly indicate the eustatic factor, whilst the '25 ft.' raised beach of Scotland and northern Ireland tilted southwards to disappear along a hinge-line across central England and Wales, sufficiently illustrates the isostatic recovery (Fig. 4). We may indeed go further and cite the evidence, suggestive but not conclusive, derived from levelling and tide-gauge records (Ordnance Survey, 1932) which indicates that even to-day the land south of this hinge-line is suffering submergence, that north of it, elevation. We may, with Wright and Scandinavian geologists, agree that the time needed for the formation of the '25 ft.' beach can most reasonably be provided by assuming that it corresponded with the rather long time during which isostatic recovery was roughly equalled by the eustatic rise, an assumption which, it must be remarked, means that the beach is not strictly of the same age along its length, but according to the principle mentioned above, must be younger in the south and older in the north.

II. BRITISH COASTAL PEATS

(i) *South coast*

It has long been apparent that the southern coast of England owes some of its salient features to the fact that it is a drowned coastline. The shallow branching harbours between Southampton and Chichester, Poole Harbour, and Romney Marsh unfailingly indicate marine transgression, which is shown again in the west by the steep-sided alluvium-filled valleys of south Cornwall and Devon. And indeed we also have direct evidence of submerged peat beds all along this coast, for instance, near Hastings at Pegwell Bay, at 50 ft. below high-tide level in the boring for the Horse Sand Fort in Spithead, at the Southampton Docks, in Poole Harbour, and Sidmouth, St Austell Bay, and in Mount's Bay.

One of the earliest of these deposits to be investigated pollen analytically was the deep bed of peat exposed at Southampton in the excavation of the great King George V graving dock (H. & M. E. Godwin, 1940). Not until the merest fragment of the deposits remained was this site visited, and greater experience would have profited more from what was available. The pollen diagram (Fig. 5) showed beyond doubt, however, that here, above the Bracklesham beds, peat formation had been continuous since the early post-glacial period: the high willow percentages, pollen of *Myriophyllum alterniflorum*, and the general forest composition dominated by pine and birch to the almost total exclusion of other trees, all supported this dating for the bottom peat, now lying about −20·0 ft. (6·1 m.) O.D. The diagram was continuous upwards through 14 ft. of fresh-water deposits and in the bottom 4 ft. zones IV, V and VI of the English pollen series are clearly recognizable. Of the uppermost 10 ft. it is not possible to state more than that it is later than this in date. Evidently, however, not until at least a late stage of zone VII did marine transgression affect levels now at −6·2 ft. (1·9 m.) in Southampton, and we must recognize that alder roots penetrating the top clayey peat indicate that some higher layers may also have been removed by erosion. Discovery of a round hammerstone in the Ocean Dock excavation unfortunately does not help to a closer dating of these strata, but that beds of similar age lie awaiting investigation in the adjacent river valleys is certain. Mr O. G. S. Crawford recently sent me a sample of peat taken out of a bomb crater in the Test valley near Nursling, and it gave the following percentage composition on analysis: *Pi* 29, *Be* 18, *Ul* 6, *Q* 47, *Ti* 0, *Al* 0, *Co* 36, *Sa* 17. This is fairly certainly referable to zone VI.

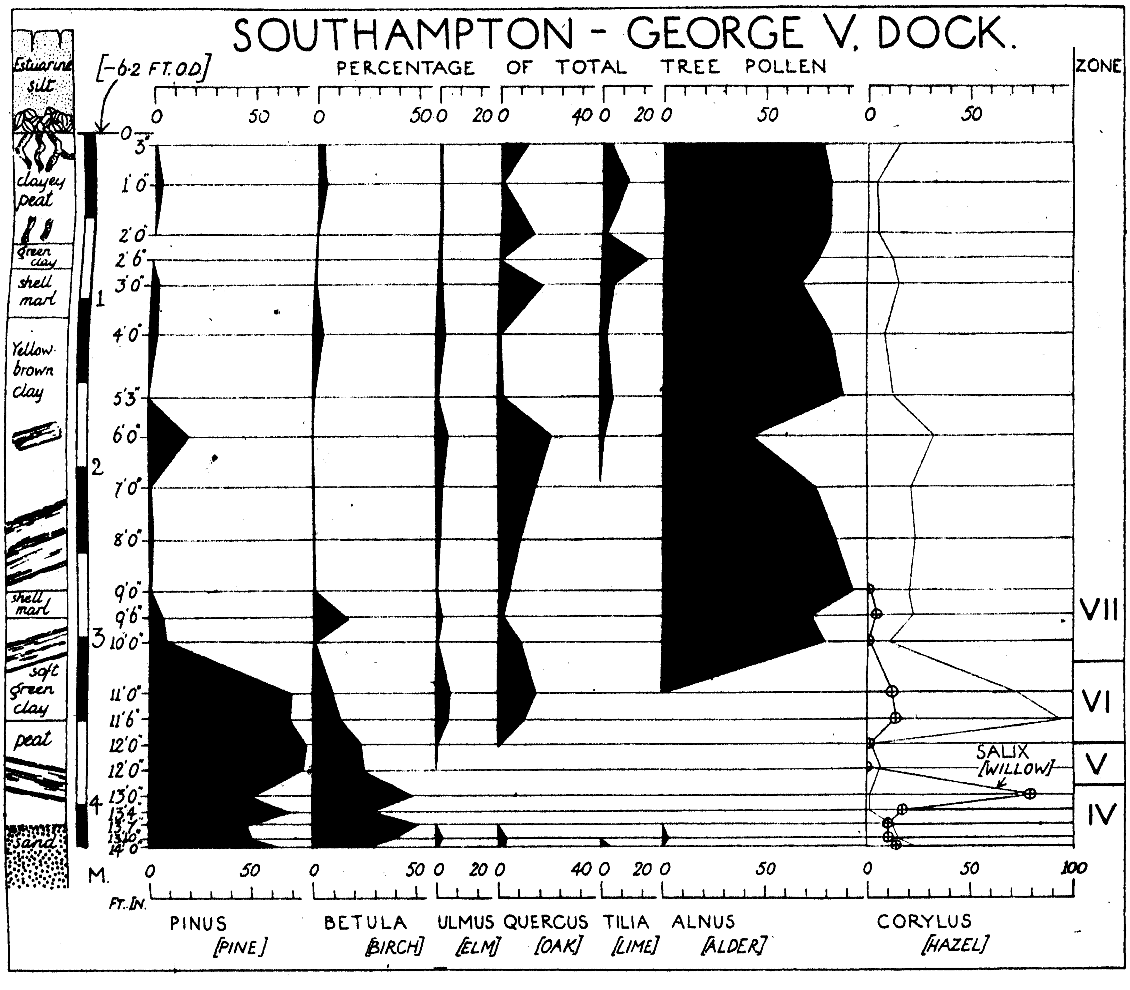

Fig. 5. Pollen diagram from George V Graving Dock, Southampton, indicating freedom from marine transgression (at these levels) until late in zone VII.

For a somewhat closer dating of the land- and sea-level movement it would clearly be best to discover and analyse also peat deposits *over* clays of the transgression period, but these have not so far been investigated, though no doubt they lie close at hand. At the same time evidence of similar kind can be had less than 40 miles to the east at Amberley Wild Brooks. Here, immediately within the Weald where the River Arun enters the Arun Gap, is a considerable tract of alluvium bearing aquatic vegetation and long known to Sussex naturalists. Dr Clapham and I discovered the centre of the region to be a derelict raised bog, and borings soon showed this to rest upon an extensive deposit of clay filling the basin to a level of about +3 to +8 ft. O.D. (Fig. 6). In one boring this clay extended down to about −8 ft. O.D., and it seems therefore reasonable to accept it as indicative of the marine transgression which ended the peat series at Southampton. Here at Amberley Wild Brooks a long pollen series overlies the clay. This pollen diagram (Fig. 7) shows a number of very clear features of change in pollen composition at the 225 cm. level: here *Tilia* alters from frequent to rare, *Betula* begins a very considerable rise which the stratigraphy does not indicate due to birches growing on the bog itself, and *Pinus* is less abundant above this horizon. Although the bog lies under the scarp of the South Downs where now rich beech-woods clothe the chalk, it will be noticed that *Fagus* is present in small amounts only until after the birch maximum. Although close and final dating is not possible, it would seem probable that the 225 cm. level which is close to the top of the clay, lies about the transition between zones VII and VIII, which in the Fenland corresponds with the Iron Age. We might tentatively place the end of zone VII at 280 cm., and the opening of zone VIII at 150 cm. The Arun, now somewhat straightened, still carries some tidal silt over flat parts of Amberley Wild Brooks which lie at +8 ft. O.D., so that we may claim to have given a rather recent dating for the end of a marine transgression on the south coast which brought the sea more or less to its present level. Prehistoric monoxylous boats have been found in the clay of the Arun Gap, but these cannot be accurately dated, and it is altogether apparent that here as at Southampton and along the south coast as a whole, we need to be more closely informed of the detailed local stratigraphy and local tree-pollen sequences for the course of marine transgression and retrogression to become clear. We should particularly welcome samples from the beds now deeply submerged in Spithead and off the Cornish coast.

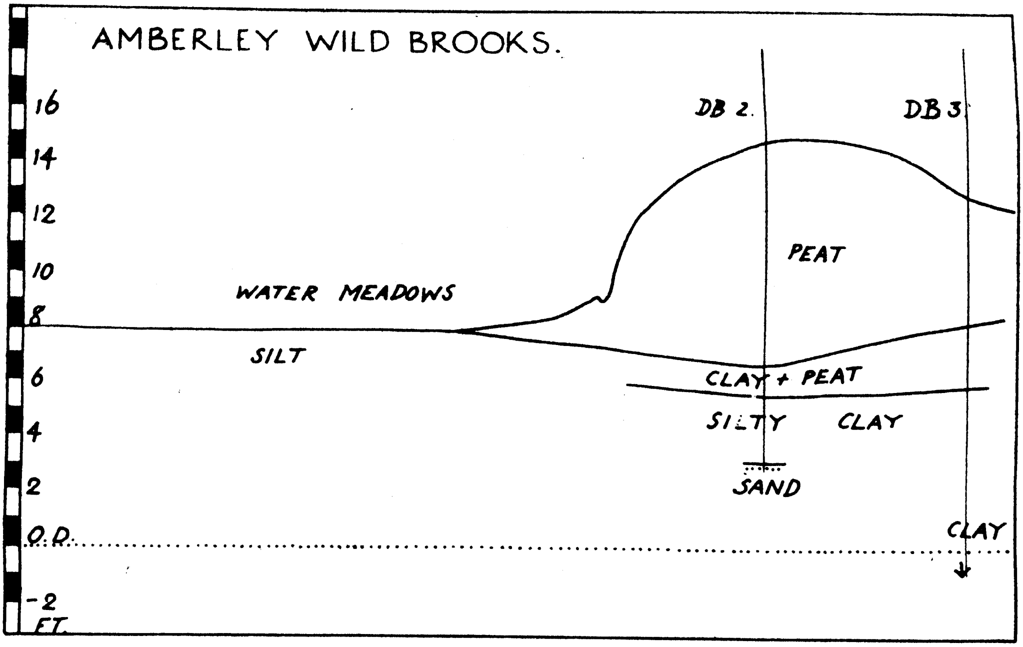

Fig. 6. Profile of the derelict raised bog at Amberley Wild Brooks, Sussex, in the valley of the River Arun.

The peat beds in the harbour of St Helier, Jersey (Figs. 8, 9) indicate a transgression later than zone VI, and this is confirmed by the evidence of the well-known submerged megalithic structures on the coast of Brittany. In the harbour at St Helier there is exposed at very low tide a thick peat bed from which oak leaves or acorns have been recovered. The strong preponderance of *Quercus* and *Corylus* pollen at the base of this peat suggests dry fen wood which, towards the top of the bed, was replaced by wet alder fen wood. The great preponderance of alder pollen at the top of this peat, now some 9 ft. (2·75 m.) below sea-level, is repeated in the series from a silty peat recovered from a boring in the Fishmarket, St Helier. The base of this series, shown in Fig. 9, is at about +3 ft. (1 m.) O.D., and it may well be of similar age to the upper part of the harbour series. Also from the coastal plain at St Helier come the two samples whose analyses are given below. They represent two peats separated by a marine layer:

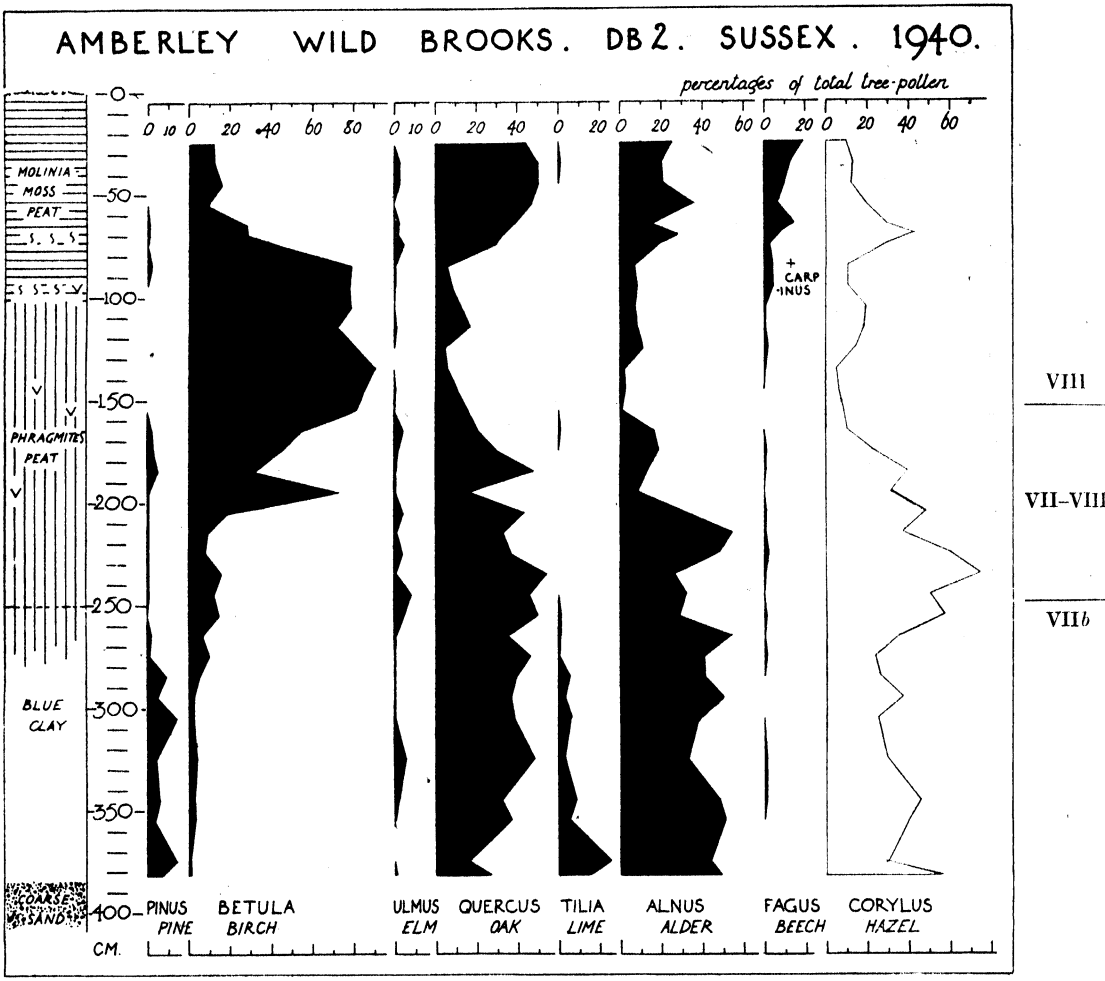

Fig. 7. Pollen diagram from bog on Amberley Wild Brooks. The transition from estuarine clay to *Phragmites* peat appears to fall about the opening of zone VII–VIII.

Amusement Arcade, St Helier

	Pi	*Be*	*Ul*	*Q*	*Ti*	*Al*	*Fa*	*Co*
No. 2 (2·15 m.)	6	6	0	42	2	42	2	64
No. 4 (2·85 m.)	0	2	2	5	1	90	0	25

The lower sample resembles those from the Fishmarket series, but the upper shows revertence from dominance by alder, slight increase in pine and birch, and 2% of beech.

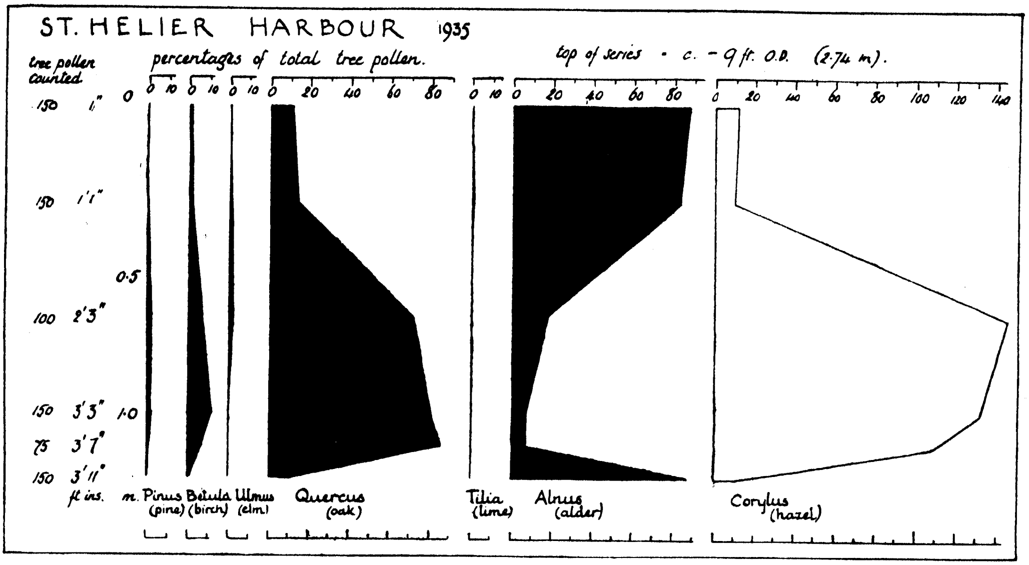

Fig. 8. Pollen diagram from the peat bed in the harbour at St Helier, Jersey, Channel Isles. Local influences preponderate in the diagram.

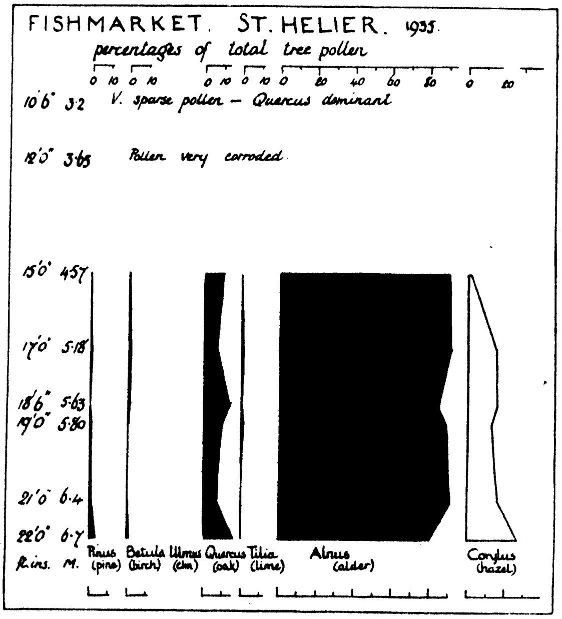

Fig. 9. Pollen diagram from borings on the coastal terrace at Fishmarket, St Helier, Jersey, Channel Islands. Note preponderance of alder growing *in situ*.

These facts suggest a peat younger than the other St Helier peats mentioned, and possibly of the same age as the upper part of the Amberley Wild Brooks series. For the samples from which these analyses were made I am indebted to Mr A. E. Mourant.

(ii) *West coast*

Opportunities for the investigation of coastal peats are numerous and good along the western shores of England and Wales, but only in three regions have pollen analyses been linked to detailed examination of stratigraphy of the coastal lowlands. Of these the first is the Somerset Levels, concerning which a preliminary account has already been published (Godwin, 1941*a*). The levels are a great lowland area on the southern side of the Severn estuary where the successive ridges of the Quantock, Polden, Mendip and Cotswold Hills run north-west to meet the coast more or less at right angles. The deep valleys

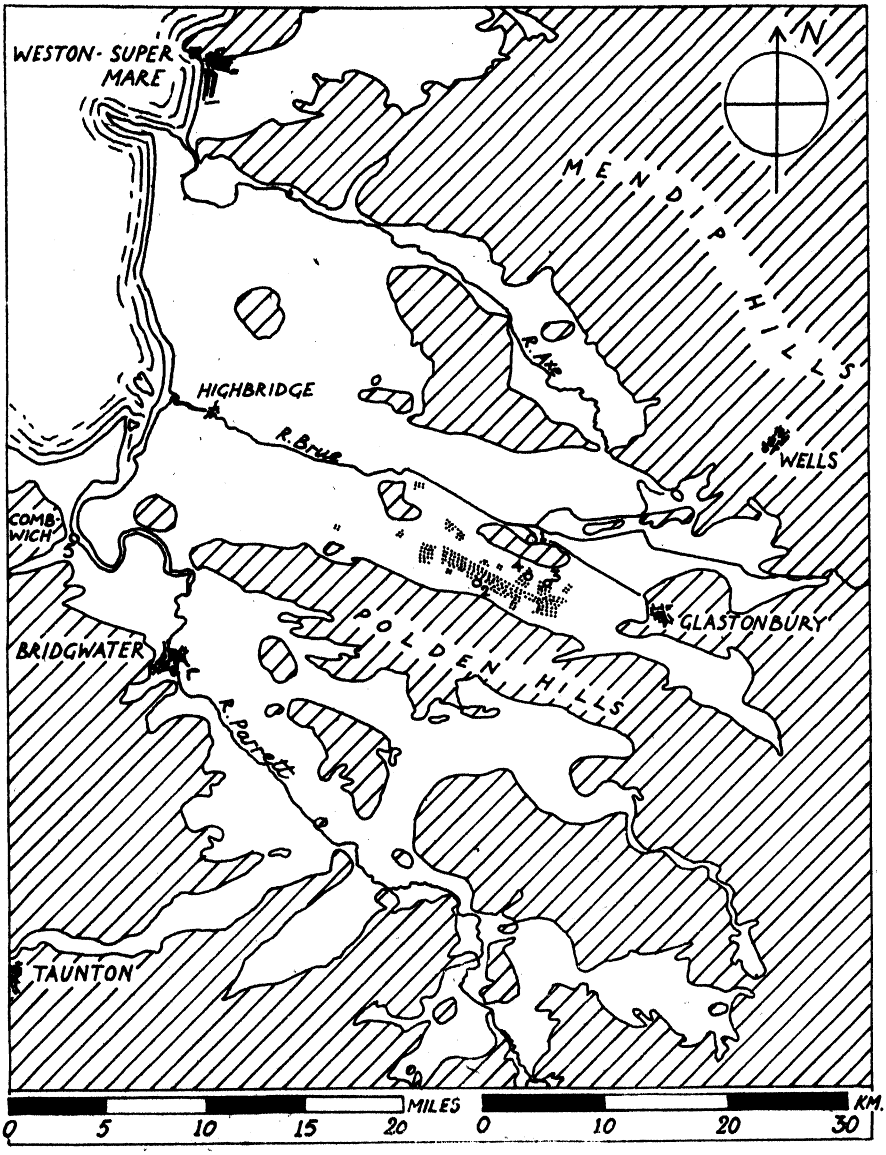

Fig. 10. Map showing the greater part of the Somerset Levels. The dotted areas are relict raised bogs. The numbered circle 2 is the site of the Shapwick Heath pollen diagram (Fig. 11). The long profile of Fig. 12 extends from Shapwick Heath east-north-east to the sea south of Highbridge.

between these hills, during the course of post-glacial marine transgression, have become filled with alluvial deposits to make the series of rather disconnected flat plains now spoken of as the 'levels'. My own investigations primarily concern the section between the Polden Hills and the Wedmore Ridge now drained by the River Brue. The seaward part of the area is a belt of clay, 5 miles or so in width, and built up to about the level of present mean spring-tide high water, that is, about 18–20 ft. O.D. Behind this is an extensive peat land, mostly cultivated, but still containing the relics of some large raised bogs which are very extensively exploited by peat-cutting. These are indicated in Fig. 10.

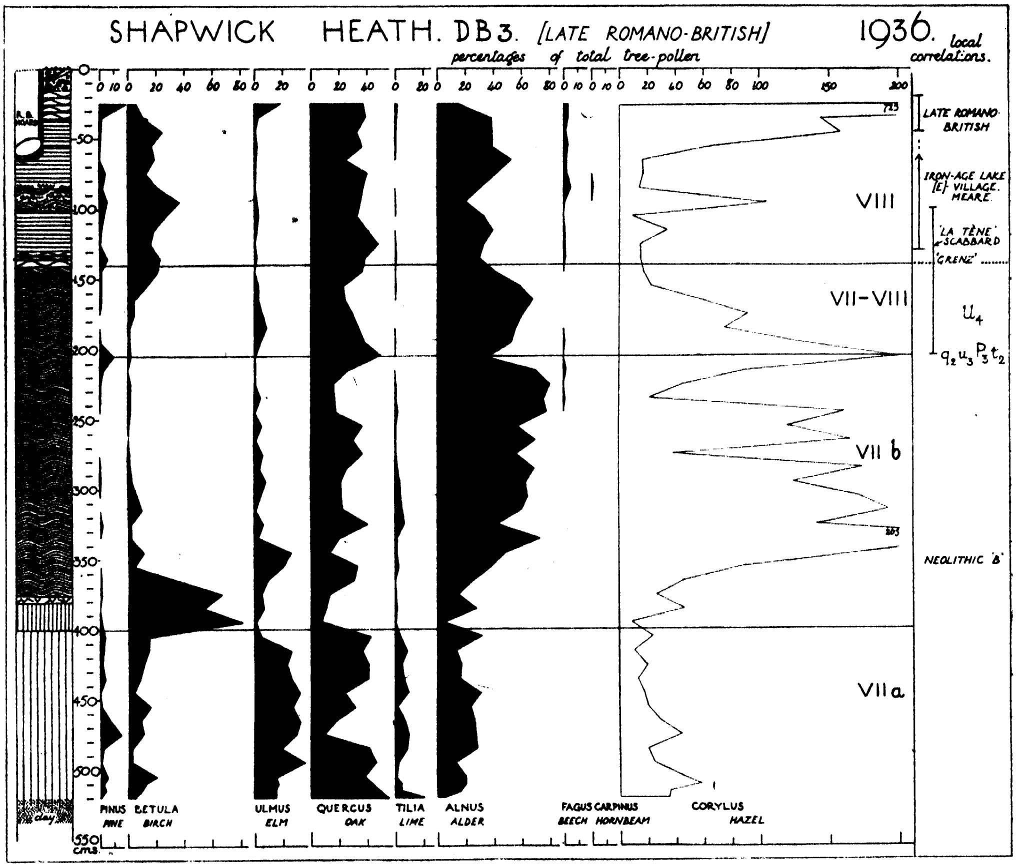

Fig. 11. Pollen diagram from Shapwick Heath, Somerset, at site of a late Romano-British hoard. Other archaeological horizons have been transferred to this diagram from discoveries in adjacent profiles. The pollen zones are those applied to England and Wales (Godwin, 1940*c*).

Borings through these peat bogs have shown that they rest upon the fairly flat surface of a deep clay, the surface of which now lies at approximately 0 to +3·0 ft. O.D. Diatom and foraminiferal analyses clearly indicate that the clay was laid down under marine influence and there is good reason to regard it as the product of a great marine transgression which filled the valleys of the Levels almost to their present extent. It is therefore very gratifying to find the big raised bogs above the clay yield long and characteristic pollen diagrams, and that in many instances archaeological horizons can be tied into the sequence of bog stratigraphy and pollen zonation (Godwin, 1941 *a*). This is very clearly indicated in the Shapwick Heath diagram (Fig. 11). Here we may clearly recognize the English pollen zones VII*a*, VII*b*, VII–VIII, and VIII. The opening of zone VIII corresponds with a clear demonstration in the bog stratigraphy of the 'Boundary-horizon' or 'Grenzhorizont', and from the surface position of several associated Romano-British hoards it is clear that bog growth ceased at about that time. In the Shapwick diagram it is not clear how far into zone VII*a* the clay deposition extended, but in a profile from Meare Heath close by the top of the clay corresponds almost exactly with the transition from zone VI*c* to VII*a*.

Several long profiles from the Somerset Levels have been analysed, and in all of them there is a striking correspondence between the stratigraphic horizons and alterations in the drift of the pollen curves. Especially is this so at the transition from a *Phragmites* or fen-wood peat to the old *Sphagnum-Calluna* peat, and it is necessary therefore to ask how far the correspondence is due to the changed conditions of the bogs directly causing the local tree growth to alter, and how far both the growth of peat mires and the composition of the pollen rain were under control by the great common factor of climatic change. Against the first alternative the following facts speak: (1) this horizon is characterized by an increase from only moderate to preponderant values of alder pollen, but one would have thought that in the fen woods below this horizon were ideal conditions for the growth of alder, and above it much less favourable ones; (2) the horizon is also characterized by a permanent diminution in values of *Ulmus* pollen, although the elm is not a tree of the Fenland itself and could not be affected by the changed edaphic conditions of the levels; moreover, its diminution at this stage in post-glacial history can be recognized in many other parts of this country and even beyond; (3) in less degree what has been said of *Ulmus* applies to *Tilia*.

It is no weakening of the case to admit that without doubt the high *Betula* values are largely or entirely due to the fen woods which flourished before the horizon under discussion, and equally the sudden rise in pollen of *Corylus* type is very probably due to *Myrica gale* growing on the raised-bog surface.

The implication thus derived that a common climatic cause led to widespread ombrogenous peat formation in the Somerset Levels, to recession of *Ulmus* and *Tilia* and to expansion of *Alnus* to a position of primary importance, forces us to consider what kind of climatic change this can possibly have been. The change can hardly have been merely one of increasing oceanicity, for it is precisely the oceanic parts of England and Ireland itself which show the restriction of *Alnus* in zone VII*a*, despite the expectation that the prevalent wetness would offer optimal edaphic conditions to this tree. Moreover, the elm is restricted at this horizon, and this tree does show a positive response to increasing oceanicity, being in zone VII*a* far more abundant in western England than in the east, and in Ireland being particularly abundant. Moreover, increased rainfall would surely have kept the levels flooded with highly basic water, and on this score alone we may perhaps reckon that it was possibly *diminished* oceanicity that caused ombrogenous peat to form and the woodlands to alter composition. Nor, considering that this horizon is not far from the Neolithic in age, would this conflict with the view that here began that climatic period, the sub-Boreal of Blytt and Sernander, which was supposed to show increased continentality after the oceanic Atlantic period.

This speculation naturally does nothing to solve the problem of how such a change operated to affect the frequency of *Alnus*, and for this one can only await a better knowledge of the autecology of this tree.

The stratigraphic relations of the Levels have recently been much clarified by the cutting of a deep drainage channel, the Huntspill River, which passes from the edge of the peat land straight through the clay belt to the sea, disclosing extremely informative sections. Miss W. Abery has made careful records and collections for analysis along the cut, and the Somerset Rivers Catchment Board have not only given access to the cut, but have allowed us the use of their initial records of boring and levelling. Subsequently, with the help of Dr Clapham, it was found possible to make a series of levelled borings to link the Drainage Cut profile with the Shapwick-Meare region already investigated, thus providing a long continuous section extending some 10 miles inland from the coast. This is given in Fig. 12. From this it is evident that the deposits of the Levels make a straightforward stratigraphic pattern. The raised-bog peats extend continuously seawards to the edge of the upper clay belt, and thence persist below it for some 2 miles. Beneath these peats the surface of the deep clay persists at about Ordnance Datum, and at one point (Witchey Bridge) it includes a peat bed some 2 ft. (0·6 m.) in thickness at a level about 13–14 ft. (4·0–4·3 m.) below sea-level. The peat bed terminates at the seaward end in a series of deep channels which are almost certainly erosion channels, and farther west still the fresh-water phase is represented only by two rather thin detritus muds (as in the section at Puriton Drove). There can be no doubt that the great extension of peat between the clays reflects a long period of freedom from marine influence between two stages of marine transgression, and we look to investigations of the peat to date these important events. Pollen analyses have indeed been made at several points along the Huntspill Cut, but here it will suffice to mention only two. At Newlands Rhyne (see Fig. 13) the upper surface of the deep clay lies at about +1·0 ft. (0·3 m.) O.D., and the high pine and low alder values indicate clearly that it is referable to the end of zone VI*c*. It is interesting to find this agreement with the dating from Meare Heath, and this is confirmed by analysis at Witchey Bridge. Here samples extended from the detritus mud at the base of the peat, through the clay and into the lower peat bed. The whole of this was seen to fall into zone VI*c*, thus indicating quite clearly that the closing stages of the lower clay transgression were taking place within this period. At Newlands Rhyne the sequence above the lower clay is the usual one of detritus mud, *Phragmites* peat passing into wood peats, and thence humified and compressed *Sphagnum-Calluna* peat. As before, the boundary between zones VII*a* and VII*b* falls at the base of the ombrogenous peat. We have not so far been able to detect the 'Grenzhorizont' in the profile, but the pollen curves suggest that it lies about the 30 cm. level. Our dating of the onset of the second transgression is fortunately simplified by the fact that on the peat surface, but below the upper clay, there are found at Newlands Rhyne, as well as at other sites along the cut, traces of the same Romano-British occupation to which Bulleid (1914) has drawn attention upon the surface of the adjacent peat land. It will, moreover, be recalled that Roman remains were found on the peat surface at Bason Bridge below 12 ft. of clay (3·65 m.) and under 7 ft. of clay at Highbridge. Thus the onset of the second transgression seems clearly dated, and we may recall that at Combwich on the mouth of the Parrett, what appears to be the same upper clay, at a height of 21 ft. (6·4 m.) O.D., has a Romano-British occupation at or close beneath its *surface*. There would thus seem to be grounds for thinking that the transgression began *and* ended within this restricted period. As to the actual height of sea-level during the long period of freedom from marine influence after the close of zone VII, we have no exact information, but here and there, there are

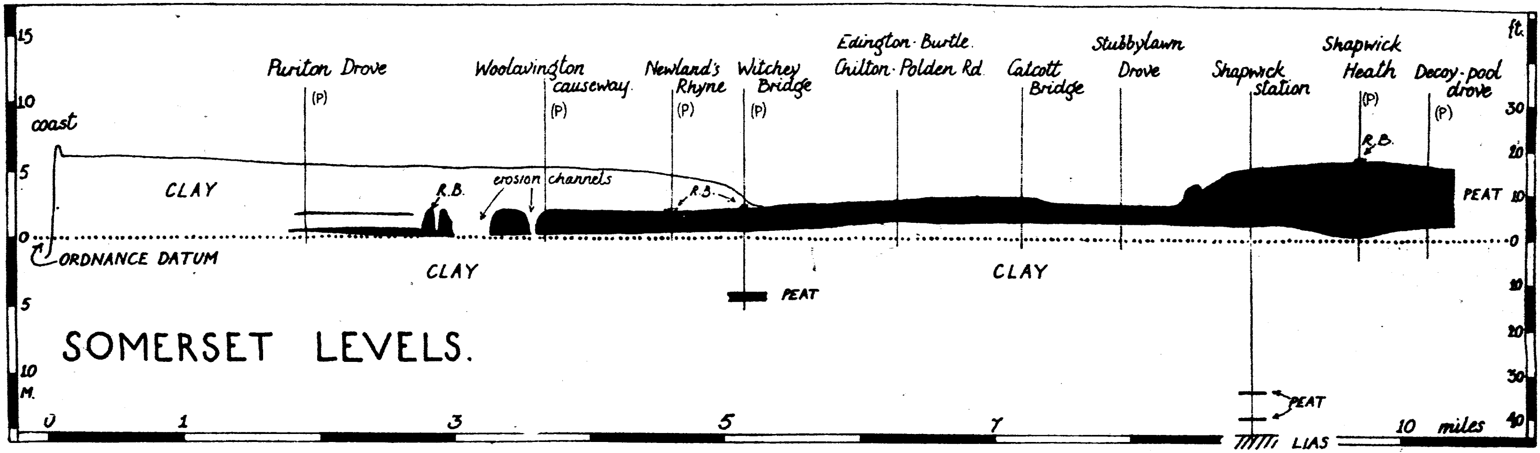

Fig. 12. Schematic profile from the Somerset coast, inland to the region of relict raised bogs. Thick ombrogenous peat extends seawards below the coastal clay belt for about 2 miles, and has Romano-British remains on its surface. The raised-bog system lies on an estuarine clay surface now a few feet above mean sea-level. Based on borings by the Somerset Rivers Catchment Board, by the author and Dr A. R. Clapham, and on field observations by W. Abery.

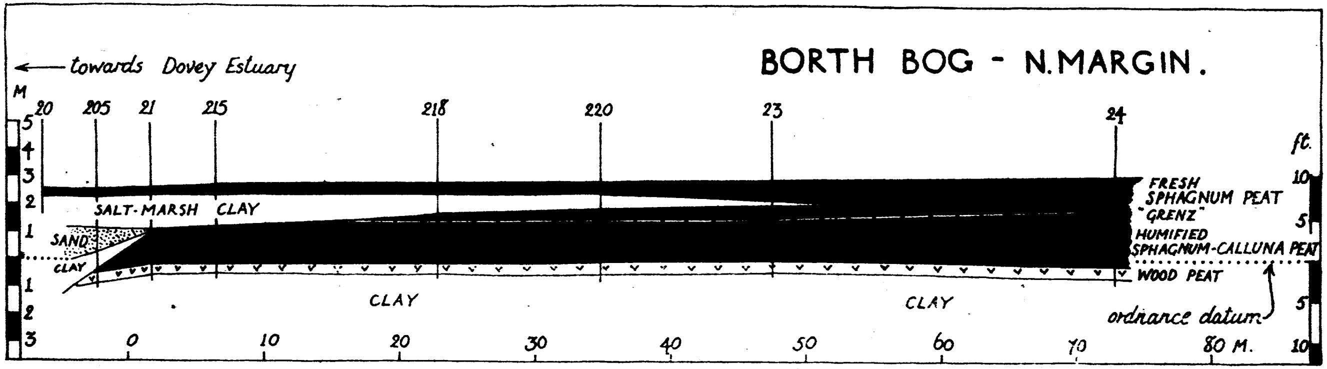

Fig. 15. Profile of Borth Bog at its northern junction with the belt of coastal silt which fringes the Dovey estuary. The base of the bog is a well-developed wood-peat layer with abundant pine-stools, resting upon estuarine clay. A later marine incursion is represented by a wedge of saltmarsh peat with *Juncus maritimus* included in the raised-bog peat above the 'Grenzhorizont'. Borings by the author and Dr D. H. Valentine.

indications that it may have remained high for part at least of the time. Thus in the Newlands Rhyne profile there is a thin band of clay just at the base of the ombrogenous peat, i.e. the end of zone VII*a*, but it has not been recorded elsewhere along the cut.

We may conclude by saying that the Somerset evidence here briefly indicated demonstrates a phase of extensive marine transgression ending at the conclusion of zone VI*c*, a long period of freedom from marine invasion through the Neolithic, Bronze and Iron Ages, and finally a stage of marine transgression in Romano-British times which brought about approximately present-day land- and sea-level relations. We may notice that these observations contradict Clement Reid's conclusion from the evidence of a causeway to the lakeside at the pre-Roman Iron Age lake settlement at Glastonbury, that, since that time, 'no measurable change of sea-level has taken place in the south of England'.

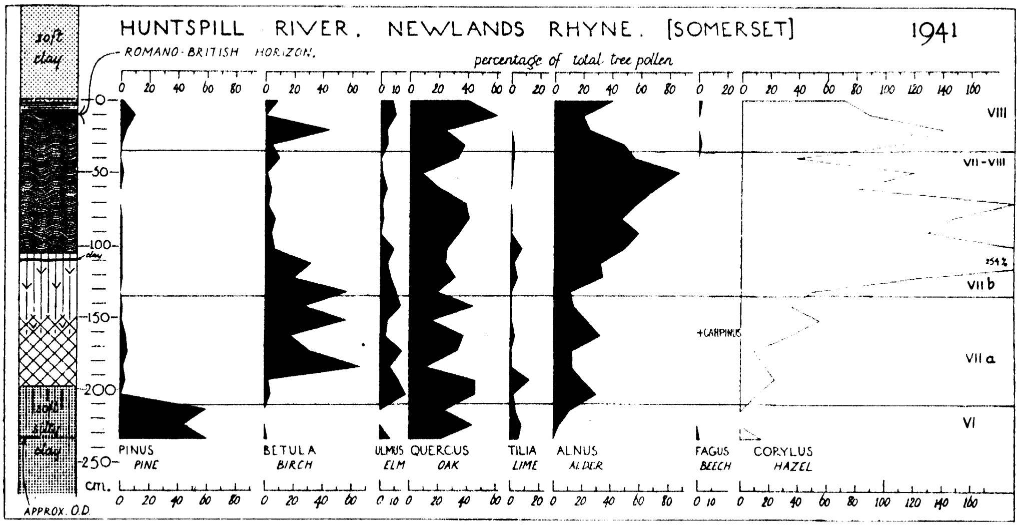

Fig. 13. Pollen diagram from Newlands Rhyne on the Huntspill Cut, Somerset. Beneath the coastal clay is thick *Sphagnum-Calluna* peat, with Romano-British occupation traces at its surface. Below this lie woody *Phragmites* peat, detritus peat, and soft estuarine clay. Zones as in Fig. 11.

On other parts of the shores of south-west England coastal peats may be found, as at Westward Ho! and at Westbury-on-Severn, but they are too fragmentary to tell us much. Across the Bristol Channel, however, along the coast of south Wales there are many instructive occurrences of such beds. Notably useful were a series of deep borings made in Swansea Bay which passed through several peaty layers, samples of which were sent to me for analysis by Prof. O. T. Jones (Godwin, 1940*b*). Jones has shown that all these deposits lie in the ancient channel of the River Tawe, which extends down to at least 200 ft. (61 m.) below present sea-level. These peats occurred as low as 54 ft. (16·4 m.) below O.D., and they all proved surprisingly readily datable by their pollen content. Those beds between −54 ft. (16·4 m.) and −28 ft. (8·5 m.) O.D. belong to zone VI*b*, and those at −20 ft. (6·1 m.) O.D. to zone VI*c*. Thus very rapid transgression must have been in progress during at least the second half of zone VI, the rate being of the order of 5 ft. (1·5 m.) per century. It is not clear when or how this phase of swift transgression ended, but peat beds exposed at about −5 ft. (1·5 m.) O.D. are referable to zone VII, and only a few feet higher are coastal peats belonging to zone VIII. It is, however, apparent that the pace of transgression slackened a great deal after zone VI, and indeed possibly some retrogression occurred.

These results are in remarkable agreement with those from the Somerset Levels, supplying evidence, however, of the deeper and earlier stages not yet recovered in Somerset. They have, moreover, been supplemented by the results of analyses of Foraminifera from the same samples that were pollen analysed. Although these samples were small and from the least marine parts of the bores, Dr W. A. Macfadyen nevertheless obtained from them a very rich fauna of no less than 127 species of presumed indigenous Foraminifera (Macfadyen, 1942). Of these Macfadyen writes: '24 species are more at home in warmer water, 6 species in colder water, and 13 species in deeper water.' The list includes, from two beds respectively at −18 ft. (5·5 m.) to −20 ft. (6·1 m.), and at −26 ft. (7·9 m.) to −29 ft. (8·8 m.) O.D., 'species not recognizable as British residents, but indicative of the warmer conditions of the West Indies, though one or two might have come from the area of the Canary Islands'. He adds that the Foraminifera 'would seem to indicate some considerable mixing of faunas, probably by ocean currents, to give a predominance of warmer over colder forms. Nevertheless too much weight must not be given to these indications, since nearly all of the thirty-seven species concerned are recorded, many as common, from British seas.' This indication of conditions warmer than those of to-day in zones VI*b* and VI*c* deserves to be borne closely in mind in view of other similar evidence of a post-glacial temperature optimum in other parts of this country and of the continent.

There are many features which suggest that closer study of the Swansea Bay deposits would be amply repaid. Thus the two peat beds at −50 ft. (15·2 m.) O.D. from boreholes 37 and 38 have been tentatively referred to the early post-glacial zones IV and V, before the expansion of the warmth-demanding trees, but if this is correct it may well imply marine retrogression between their deposition and that of the marine series in the other bores. The evidence is, however, weakened by the fact that abundant birch bark in the peat samples may provide a merely local explanation of the great preponderance of birch pollen in them. Furthermore, behind a fringe of dunes lies the great Crymlyn Bog, the base of which may very well actually be part of the series of submerged peats in the Bay, and detailed examination of the stratigraphy of the bog, with suitable analyses, could be counted on to reveal much of the later history of land- and sea-level movement of this region. Apropos of this it should be recalled that von Post (1933) reports the analysis of a wood peat from the beach at Blackpill in Swansea Bay. This bed lies about +10 ft. (3·05 m.) O.D., and the presence of beech pollen in four out of the five samples led von Post to refer it to the Iron Age.

At many dock excavations along the south Wales coast, peat beds have been recorded, and their occurrences correspond tolerably well with those just described. The best known series is that described by Strahan (1896) from the docks at Barry. The lowest peat there contained much wood of oak, hazel, dogwood, hawthorn and willow, an assemblage which would agree with its reference to zone VI*b* on the basis of the Swansea beds at the same depth. At −20 ft. (6·1 m.) was another peat bed with large oaks, a third layer at −10 ft. was impersistent, but at −3 ft. (0·9 m.) to −5 ft. (1·5 m.) was a fourth layer with willow, pine and oak trees. This last contained a fragment of a polished Neolithic flint celt, which if it is a true index to the age of the bed, suggests reference to the middle of zone VII. It will be recalled that in Somerset at this time wood peat or the early ombrogenous peat was forming. This site on the coast of south Wales was so situated that it evidently did not experience the long period of freedom from marine influence seen in the Somerset deposits, and so seems to indicate that no very long or extensive fall in sea-level took place during this time.

At East Moors, Cardiff, Hyde (1936) has given analyses through coast peats lying from about −0·5 ft. (0·15 m.) to +12·5 ft. (3·8 m.) O.D. These beds are full of wood, so that local effects colour the pollen diagrams, whilst abnormally high values of *Tilia* must also be due to some local source. Nevertheless, the bed is probably referable to the later part of zone VII and the early part of zone VIII, in conformity with the age of beds at similar levels farther west.

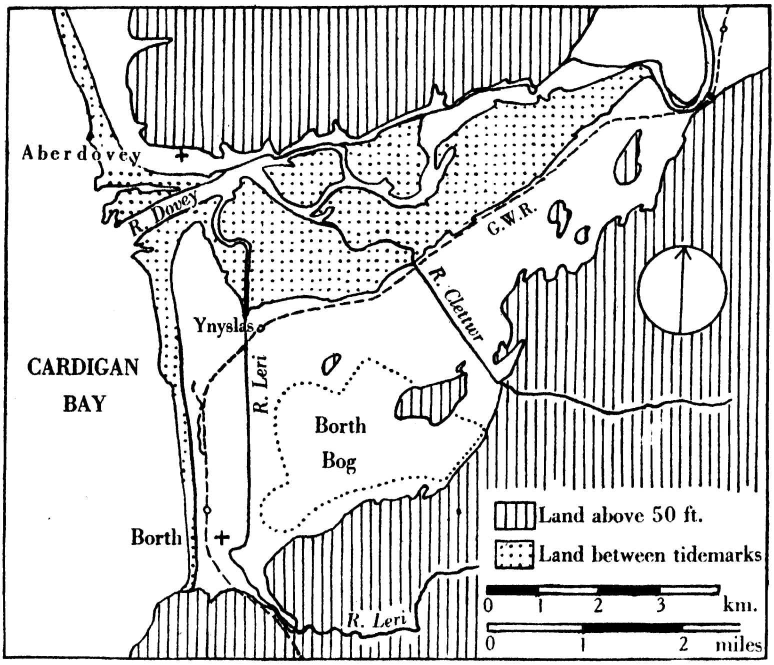

Fig. 14. Sketch-map of the Dovey estuary, Cardiganshire. Shore peats occur at Borth and Ynyslas. These are laterally continuous with the great raised bog (Borth Bog) which lies inland, separated from the sea by a big shingle-spit. The profile in Fig. 15 runs north and south across the northern bog margin nearly parallel with the River Leri and about ½ mile to the east of it.

We have already, on p. 203, said something of the stratigraphy of the submerged peat on the beach at Ynyslas, just north of Aberystwyth, and of the relation of this peat to that of the great raised bog, Cors Fochno, or Borth Bog, which is enclosed in a big triangle by the shore of Cardigan Bay on the west, by the Dovey Estuary on the north, and by steep hills on the south-east (see Fig. 14). It has now been possible to secure a complete levelled line of borings from north to south across the bog (Fig. 15) and also an east-west line linking the first section to the beach exposures at Ynyslas. These sections reveal the very striking fact that coastal peat and all the bog rest upon a flat surface of blue clay at a level approximately −2·0 ft. (0·6 m.) O.D. Foraminiferal analyses of this clay kindly made by Dr Macfadyen showed that its surface was formed in brackish water conditions. Attempts to bore through it met neither deeper peat nor hard rock. Everywhere along the profile, save the extreme margins, the bog showed a similar stratigraphy: above the blue clay a thin *Phragmites* peat gave place to a well-developed wood layer, and this was then directly succeeded by several feet of very humified *Sphagnum-Calluna* peat. The twofold division of the ombrogenous peat found in so many raised bogs was here difficult to recognize, for the upper half of the peat was more humified than is usually the case, although at the same time much more banded with layers of fresh peat than the lower half. The indication of the Boundary Horizon in the profile of Fig. 15 is therefore only provisional. It appears that the bog growth has continued to the present day, and pollen

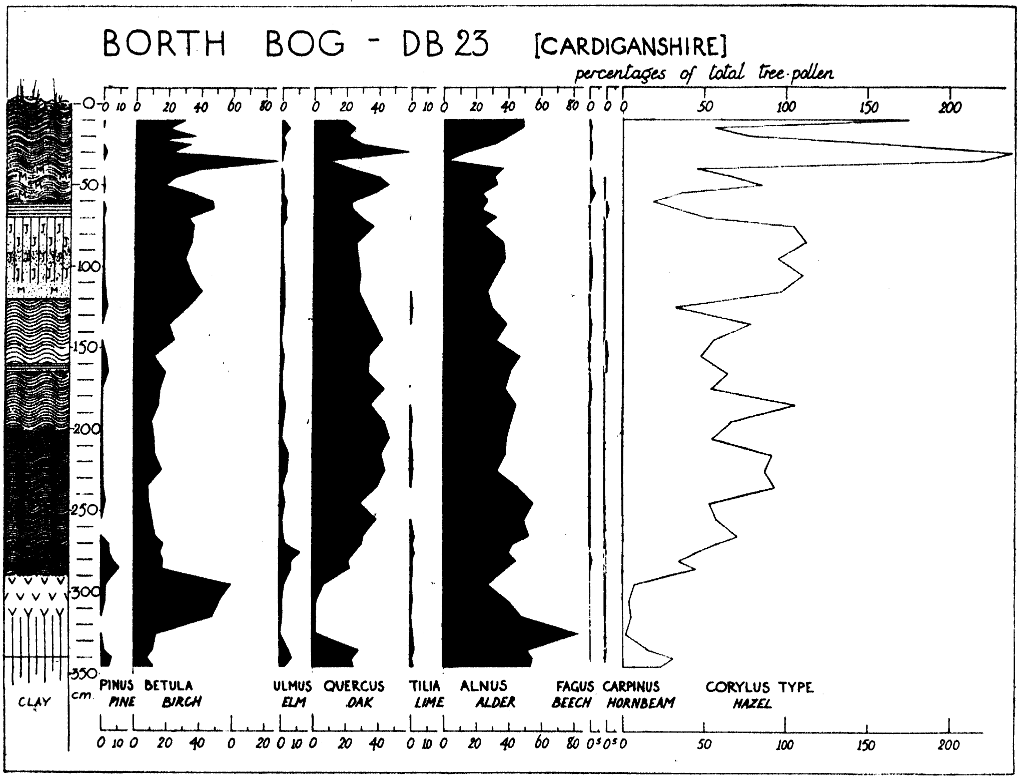

Fig. 16. Pollen diagram through Borth Bog, Cardiganshire. The degree of humification of the *Sphagnum-Calluna* peat is indicated by the closeness of the wavy lines. This peat is interrupted by silty *Juncus maritimus* peat, and rests on wood peat which induces local effects in the pine and birch curves of the diagram. The presumed 'Grenzhorizont' lies at about 160 cm.

profiles were obtained through the complete thickness of the bog in two places. One, not here reproduced, was in the centre of the bog, the other DB 23 (Fig. 16) was near the northern bog margin, where it crossed the landwards extremity of a very interesting late marine deposit. This is a wedge of saltmarsh clay, here some 300 yd. long, which is full of the rather undecayed remains of *Juncus maritimus*, and which, according to Dr Macfadyen's analyses, contains a rich assemblage of purely marine Foraminifera. It will be seen from the profile (Fig. 15, p. 220) that this wedge of marine clay lies above the Boundary Horizon.

We may now consider what information as to the dating of the bog's history is given by our pollen analyses. It will be apparent at once that the base of the diagram is influenced by the local vegetational succession, displaying the same sequences of maxima of *Alnus, Betula,* and *Pinus* that was found in the shore exposures. Discounting this so far as possible, and making comparison with the long profiles at Tregaron, some 20 miles to the south (Godwin & Mitchell, 1938) and with unpublished profiles kindly lent by Dr J. B. Jones, it seems clear that ombrogenous peat formation began shortly before the transition from zone VII*a* to VII*b* (*c.* 270 cm.), and that the deep clay deposition ended between this and the end of zone VI*c*. Thus a phase of considerable marine transgression ended in zone VII*a*, and thereafter for a long time the bog growth remained unaffected by rising sea-level. There is some indication in the deposits of the old natural channel of the River Leri on the south flank of the bog, that sea-level may nevertheless have remained fairly high, but this calls for much more detailed investigation.

It is not altogether clear whereabouts the end of zone VII*b* should fall in this pollen profile; the somewhat slight stratigraphical evidence of the 'Grenze' suggests at 160 cm., the rather better pollen evidence at 125 cm. In either event the second marine stage falls early within zone VIII. Closer dating is not yet possible, nor have archaeological remains been found to bear upon the issue. Until the stratigraphy and pollen diagrams at Borth have been considered in close comparison it is not feasible to zone the diagrams nor to go beyond these general conclusions. Nevertheless, in the big phase of transgression ending in zone VII*a*, and the long period of uninterrupted bog growth until the latest incursion of zone VIII, this region accords well with the results from south Wales and Somerset.

At other places along the Welsh coast we have clear evidence of the occurrence of submerged peat beds and Jones (1921) has pointed out how intimately they are related to the rich legend of the Welsh people. We cannot say, however, how far the submergence of the fertile land, Cantref y Gwaelod, beneath the waters of Cardigan Bay, was a genuine, if modified, folk memory of an actual catastrophe, and how far a story evoked by the sight of a submerged landscape. The deepest peats from Swansea Bay are represented in Cardigan Bay by a bed encountered more than 50 ft. (15 m.) below sea-level during construction of the railway bridge at Barmouth, but it is also likely that the long 'sarns' projecting from the coast towards the Irish Sea are the ridges between the river valleys of the drowned land.

At Rhyl, on the northern coast, the submerged peats are higher in level and have yielded archaeological evidence of age. The two forest beds are separated by estuarine clay from which two Craig Llwyd axes (Late Neolithic) have been recovered, as well as a bronze chisel and bronze armlet (Morris, 1923; Glenn, 1926, 1930). Mr Glenn now informs me he has also found early Neolithic artefacts in the lower of the two peat beds. Pollen investigations by Bibby (1940) at the same place do not give a closer dating of the series, but do not disagree with it, and certainly confirm the strong local development of pine-woods in the upper bed. It is evident that the peat beds of the north coast of Wales grew in zone VII, during the long period of peat formation on Borth Bog.

Although a good deal of attention has been given by local observers to the peat beds on the Lancashire and Cheshire coasts at Hightown and Leasowe (see Travis, 1926, 1929), very little has yet emerged which will serve to date them. They lie on blue estuarine clay on the present shore, and contain abundant tree remains of *Alnus*, *Betula*, *Corylus*, *Pinus*, leaves of *Ilex aquifolia,* and pollen of *Tilia*. Rhizomes of *Osmunda regalis* are conspicuous, and the remains clearly show the rapid transgression from fresh-water marsh to fen woods, which is so common on our coastal peat beds.

We have already referred to Rankin's 'estuarine' type of raised bog, lying on the coastal plain of Lonsdale. After the episode of the marine transgression the saltmarsh surface was evidently covered by fresh-water fen, which was in turn displaced by fen woods, and these by ombrogenous *Sphagnum* peat. Here once more the 'Grenzhorizont' is apparently manifest as a boundary in the *Sphagnum* peat. Pollen analyses here are restricted to the preliminary observations published by Erdtman in 1928. He gives figures for two mosses, both of the estuarine type, and from them certain restricted conclusions may be drawn. Thus *Alnus* is prevalent through both diagrams, which must therefore evidently be later than zone VI. Some *Tilia* is present, and this confirms that the layers below the 'Grenzhorizont' belong to zone VII, whilst the considerable thickness of peat below this horizon suggests that the top of the clay must be referred to an early part of that zone.

It seems not unfair to conclude that the evidence all along the west coast of England and Wales broadly agrees in showing an extensive and rapid submergence going on in zone VI and brought to a standstill or greatly slowed down early in zone VII. The evidence for a later submergence is stronger in the southern than in the northern part of this coast.

(iii) *Scotland*

In extending the range of our survey from England and Wales to Scotland we shall experience the disadvantage of entering territory for which the post-glacial forest history is still very imperfectly known. Since Erdtman's general but preliminary survey (1924*a*, 1928) very little advance has been made, and his pollen diagrams are constructed of samples taken at what are now considered very great intervals. Scotland of course shows some of the most impressive features of post-glacial geological change, and the 100 ft. raised beach, the 25 ft. raised beach, and the carse clays have long been recognized as important indices to the relative movement of land and sea in this time. The 100 ft. beach is apparently connected with the final stage of the last glaciation (Wright, 1937; von Post, 1933), but has not so far been directly related to pollen-analysis studies in Scotland. The so-called '25 ft. raised beach' occurs over a wide area, embracing most of Scotland, the north of England, and north-eastern Ireland. It occurs at a height of about 40 ft. at a centre near Loch Linnhe, at about 50 ft. in the Tay and Upper Forth, and descends outwards from this region to intersect modern sea-level along a line (the zero isobase), which is indicated in Fig. 4.

There is now no doubt that the elevation of this shoreline, and that of the 100 ft. beach within its area, has gone on most rapidly where the ice thickness of the last glaciation was greatest, and follows from a non-uniform uplift of the earth's crust in consequence of the isostatic restoration of the earth's shape after its deformation by the ice load.

Associated with the 25 ft. beach are the estuarine deposits of the same period, the deposits of 'carse-clay' which are extensively present at the heads of the Firth of Tay and Firth of Forth. This clay forms extensive and fertile flats up to about 15 m. above sea-level and is in places more than 6 m. thick. In it are marine shells, and the skeletons of whales have been found in several places. Dug-out canoes have been recovered from it, although unfortunately these afford little indication of age. These clays commonly rest upon a peat bed, as was admirably demonstrated by Jamieson (1865), and as this bed in places contained the stools of trees, it inspired the statement that 'the 25 ft. beach is distinctly later than the submerged forest period'. The error in this view we have already pointed out. Jamieson's figures admirably illustrate the relations between the carse clays and peat beds both above and below them, and it was not lost upon Erdtman that these sites provided possible opportunity for pollen-analytic dating to be applied. He cites four investigations.

At Ochtertyre Moss he describes the sequence

A, 0–225 cm., little humified *Sphagnum* peat.
B, 225–335 cm., well humified *Sphagnum* peat.
C, 335–680+ cm., carse-clay.

Without giving the results it is said 'Pollen-statistics prove the peat to be sub-boreal, or rather, late sub-boreal and sub-atlantic. The carse-clay was thus chiefly formed previous to sub-boreal time.' We miss a stratigraphic analysis which might tell whether the boundary between A and B is, or is not, a well-developed boundary surface, and stratigraphy also might tell more of the implications of the find reported from the same bog by Munro (1906). This was a bronze cauldron actually resting upon the clay surface. Tree stumps of oak, alder, willow and hazel are reported from the peat just over the clay, some of them with axe cuts. From this lowest peat layer Erdtman also reports a pollen spectrum: *Be* 39%, *Pi* +, *Q* 8%, *Al* 53%, *Co* 18%.

Near Forgandenny, south of Perth, on the River Earn, Erdtman reports an analysis of an 18 cm. thick peat which lies below 300 cm. of carse clay. He says: 'the pollen spectra are boreal with Co (dominating), Be, Pi and Q.' He points out that although alder pollen was not found, the roots of alder have been reported below the carse clay, and speculates that possibly the uppermost peat layers may have disappeared before clay began to form. He adds that 'the carse clay is shown by pollen statistics to be Atlantic in age', and that pollen analysis supports the reference by Geikie and by Lewis of the peat below the carse clay to the Lower Forestian, a stage which Sernander (1908) and Samuelsson (1910) had already indicated as probably equivalent to the Boreal period of southern Scandinavia.

We may perhaps best summarize the scanty evidence for the age of the carse clays thus presented by saying that they formed within a period between (and perhaps partly including) that of zone VI of England and Wales, and the Bronze Age in Scotland. The desirability of and opportunity for closer investigation is apparent.

The dating of the deposits of the 25 ft. beach themselves has also been begun by Erdtman, who describes two bogs lying on the old beach, one the Moss of Cree between Newton Stewart and Wigtown, and the other Lochar Moss, farther east on the Solway Firth. The profile of the Moss of Cree reveals a birch-wood layer overlying a silty clay, and itself covered by *Sphagnum* peat some 3 m. thick, divided into a rather thicker lower portion of highly humified peat, and an upper portion of less humified peat. The boundary between the two is evidently the Boundary Horizon at the sub-Boreal sub-Atlantic transition. Erdtman gives an open pollen diagram from this bog, and this we reproduce in Fig. 17. He writes of the wood peat as 'sub-Boreal (possibly partly Atlantic)', but it is exceedingly difficult to support any close dating by the pollen data alone. The deposit began after mass extension of the alder, but how long after is hard to say, although the considerable thickness of decayed *Sphagnum* peat argues a fairly early date. It is of course true that very widespread tree layers formed in Scottish bogs in the Upper Forestian period of Geikie, which almost certainly is the equivalent of the south Scandinavian sub-Boreal period, but at any stage of expansion of raised bog over upland, forest growth may be overwhelmed. Thus wood peats at the base of raised bogs may be of any age, though certainly they will be more prevalently formed at times when climatic conditions favoured extension or renewal of bog growth.

From Lochar Moss Erdtman reports the extraordinarily deep profile below:

A (i) 0–260 cm., much decayed *Sphagnum* peat.
(ii) 260–310 cm., slightly decayed *Sphagnum* peat.
(iii) 310–460 cm., much decayed *Sphagnum* peat.
B 460–760 cm., peat with *Menyanthes*, *Cladium* and *Thelypteris*.
C 760–798 cm., clayey nekron mud.
D 798–818+ cm., rhizome-bearing grey clay.

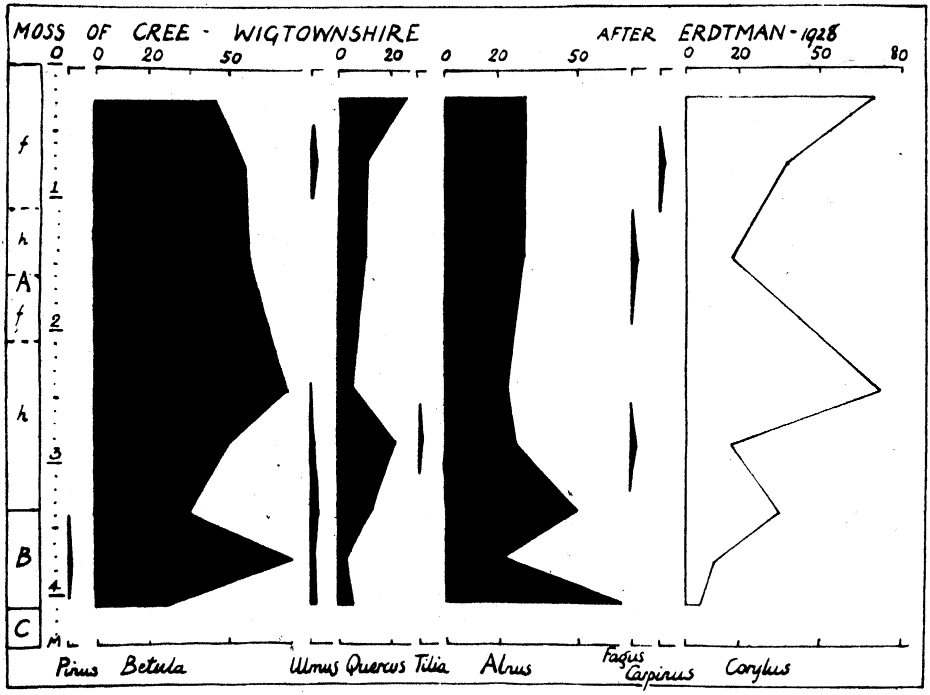

Fig. 17. Pollen diagram from the Moss of Cree, Wigtownshire (after Erdtman). *A* = raised-bog peat, *B* = wood peat, *C* = silty clay: *f* = fresh, *h* = humified peat. This peat bog lies on the 25 ft. raised beach.

A sample at 790 cm. yielded *Be* 45%, *Pi* 2%, *Ul* 3%, *Q* 29%, *Al* 21%, *Co* 15%. Although Erdtman comments that in spite of the great depth the basal peat is of the same age as in the Moss of Cree, 'chiefly sub-Boreal and sub-Atlantic', it seems to us that here also a greater age is probable, though evidently not so great as to predate the time of the alder's extension at the expense of pine and birch.

If we set aside a natural tendency to discover that the carse clays and 25 ft. beach correspond with the Scandinavian *Littorina* beaches, neither of the two Scottish manifestations can be said to have been at all closely dated by the pollen analyses, nor will this be achieved until specific research is undertaken for this purpose. Such research would, however, be very well worth while.

Meanwhile it remains to point to one further result of outstanding interest. Dr Blackburn (1940) reports briefly that the island of Soay, just off the south-west corner of Skye, provides some remarkable evidence of the maximum marine transgression. The two parts of the island are separated by a low peaty isthmus, and close beside, but at a higher level, lies a small lake containing at the bottom 9 in. (23 cm.) of fresh *Sphagnum* peat, then 1 ft. 6 in. (46 cm.) of gritty clay, a grey-brown mud of similar thickness, and then a fibrous lake deposit changing gradually at the top to a *Sphagnum* peat. The total depth was 10·5 ft. (3·2 m.). It turned out that the grey-brown mud contained abundant salt-water diatoms, an indication in all probability of the phase of marine transgression which built the section of 25 ft. raised beach present close at hand on the island. The lake mud over this deposit contains desmids, which are safe indicators of the return of fresh-water conditions. Dr Blackburn has prepared a pollen series through the whole of this sequence of deposits, and from this (Fig. 18), which she now kindly allows me to publish for the first time, it appears that the basal *Sphagnum* peat is Boreal in age (zone VI), whilst the marine clay comes in very near to the transition between zones VI and VII.* The site is fortunately placed, for it must represent the *maximum* extent of the marine transgression, which transgression would thus appear, at Skye, to have been practically completed before zone VII. We cannot, unfortunately, learn from the diagram when it was that fresh-water conditions replaced marine, for too little is yet known of the detailed drift of Scottish forest history in the latter part of the post-glacial period.

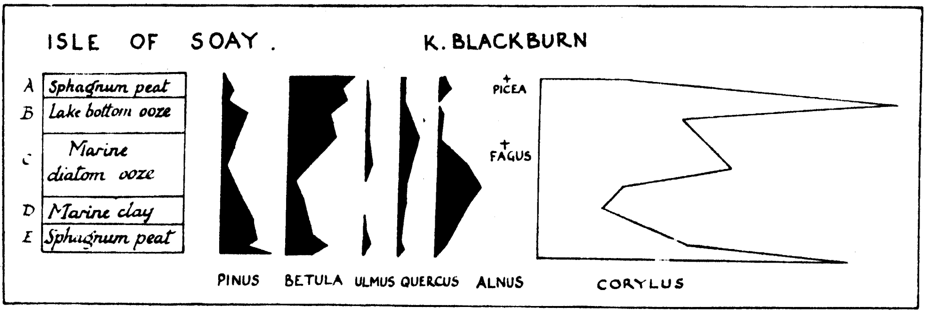

Fig. 18. Pollen diagram from data given by Dr K. B. Blackburn from the Isle of Soay, near Skye, on the isthmus in the centre of the island. Deposits C and D are presumed to represent the 25 ft. beach marine transgression.

A little further archaeological evidence exists in the Azilian shell-mounds on the 25 ft. beach at Oronsay, and Azilian remains from a cave at beach level at Oban. Unfortunately this Mesolithic culture cannot be closely dated in Scotland, particularly since it appears to lie on the very fringe of the Azilian culture area and at the same time reflects an indigenous continuation of Palaeolithic cultures (Clark, 1932).

(iv) *Ireland*

There is much submerged peat round the coasts of Ireland: it has been reported equally from the Atlantic, Irish Sea and English Channel coasts, but pollen-analytic examination has only been published for a few sites in the north-east. In north-eastern Ireland the 25 ft. raised beach is conspicuously developed and lends especial point to attempts to correlate forest history with land- and sea-level movements. Here not only are the beach deposits strikingly evident but they are associated with an immense concentration of characteristic artefacts from the prehistoric 'Larnian' culture, and in addition Lloyd Praeger (1888, 1892) has demonstrated that the period of beach formation is represented in deep excavations at Belfast harbour by marine clays, in which, indeed, he was able to make, by their content of shells, a pioneer demonstration of the post-glacial warmth maximum. In 1931 a 3 ft. (1 m.) peat bed below similar clays was found in the Milewater Dock at Belfast, and Erdtman (see Charlesworth, 1935) gave a pollen spectrum from it as follows: *Be* 50%, *Pi* 40%, *Ul* 2%, *Q* 8%, *Co* 200%. There is little reason to doubt that this sample of the peat, 31 ft. (9·5 m.) below the surface of the deposits (but of unknown relation to O.D.), is referable to zone VI of our English scale, in which hazel maxima are so strongly developed.

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* Such a determination rests a good deal on the assumption that the extension of *Alnus* was here contemporaneous with its English extension. If delayed, as in Ireland, it is possible that the reference should be to a post-Boreal zone.

Much more exact fields of reference for this region were, however, shortly to be opened. Prof. K. Jessen, with scientific assistants from Denmark and from Eire, has made an extremely wide collection of series for pollen analysis from many parts of Ireland, and has already published a tentative outline zonation of Irish pollen diagrams. Although the bulk of the data are yet unpublished it is clear that here a time scale of the utmost value is in preparation. Not only so, but Jessen has already directly collaborated in the work of the Harvard Archaeological Expedition upon the raised beaches and their prehistoric cultures (Movius, 1936, 1940). The results of this expedition are very fully dealt with by Movius in his recent book, *The Irish Stone Age* (1942).

Before, however, we can consider the results of analyses of peats and other deposits associated with the beach, it will be necessary to consider briefly how the Irish diagrams compare with those for England and Wales. This we may do on the basis of several diagrams published by Erdtman, Jessen, Mitchell and others, and particularly by a recent paper by Mitchell (1942), in which a specific comparison is attempted between a long fairly complete sequence in Co. Meath, and the general run of English and Welsh diagrams. From such comparison we note at once the absence from Ireland not only of *Fagus* and *Carpinus*, but also of *Tilia*. *Ulmus*, which tends to reach high values at various sites in the west of England, is still more abundant in the Irish diagrams, and so is *Corylus*, which often many times exceeds the total tree pollen. *Alnus*, which might be expected to be present even more abundantly in Ireland, is in fact distinctly less frequent, and its expansion much more gradual than in England. In particular this alder pollen, in failing to exhibit the sudden extension at the expense of pine and birch familiar in the English diagrams between zones VI and VII, weakens a very useful index horizon. In increasing counterweight to these difficulties may be set the active establishment of correlation between the Irish pollen diagrams and the archaeological periods, remains of which are so richly present in the Irish peat bogs.

Cushendun, Co. Antrim

Much the most important of the sites investigated by the Harvard Expedition is that at Cushendun, where the River Dun cuts through the early post-glacial terrace, 35 ft. (10·7 m.) above sea-level, on which stands the village of Cushendun itself. This site was sufficiently removed from the open sea to contain, in addition to the 25 ft. beach gravels, beds of silt laid down under quiet water. The main section was recorded as follows:

			cm.
(A)	Humus	Horizon (4)	50
(B)	Upper gravel	Horizon (3)	315
(C)	Upper lagoon silt		77
(D)	Lower gravel	Horizon (2)	358
(E)	Lower lagoon silt	Horizon (1)	46
(F)	Swamp peat		10
(G)	Resorted boulder clay		30
(H)	Laminated clay	Thickness undetermined	
(I)	Boulder clay		

The three lowest horizons in the table show abundant Mesolithic culture material in secondary position, incorporated into the beach deposits during their formation.

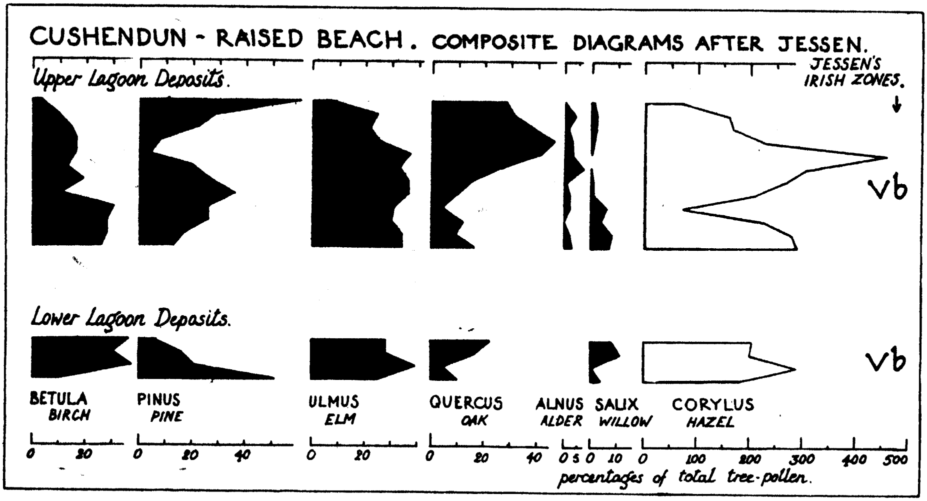

Fig. 19. Composite pollen diagrams from deposits at Cushendun, Co. Antrim, Northern Ireland formed in association with the 25 ft. raised beach. The upper lagoon deposits correspond closely to the stage of maximum marine transgression. After K. Jessen, whose Irish zonation is retained.

Horizons (1) and (2) are referred by Movius to the 'Early Larnian' culture, and horizon (3), at the maximum of the submergence, and during re-emergence is referred to the 'Late Larnian'.

Of these beds short pollen series have been obtained from the swamp peat (F), the lower lagoon silt (E), and the upper lagoon silt (C). The swamp peat was brown and laminated, containing *Phragmites*, wood debris of *Ulmus* and fruits of *Crataegus*, *Corylus*, and *Carices*. The immediately overlying lower lagoon silt (E) contained marine fossils throughout and indicated deposition in sheltered, rather estuarine conditions becoming less marine at the top. These two beds which now lie about +8 ft. (2·4 m.) to +9 ft. (2·7 m.) O.D., were deposited fairly close to mean sea-level. The joint pollen diagram for the two together is given in Fig. 19. Hazel pollen is very abundant, pine and birch though abundant are equalled by elm, oak is less frequent, and alder is absent. We can hardly do other than refer these beds to the middle of zone VI of the English schema, and in this we are supported by Jessen who places them in the *Irish* zone V*b*. He says: 'the palaeobotanical age of these deposits is given by the lack of alder, the decline of the pine curve from an extraordinarily high maximum, and a high percentage of hazel. Compared with other pollen diagrams from Northern Ireland, it appears very likely that it falls in the lower part of zone V*b*, which contains the co-called Boreal hazel maximum.'

At the maximum of the raised-beach transgression, sea-level, apparently represented by the upper lagoon silts and base of the upper gravel, was only some 15 ft. (4·6 m.) above this, and we may therefore conclude that *by the middle of English zone VI marine transgression had already come within some* 15 *ft. of its maximal vertical height.* We have already seen that in Swansea Bay there is clear proof that the last stages of a great transgression were manifest at the same time, and the analysis of deep peat from the Milewater Dock, already referred to, confirms our dating of this great submergence. That this submergence was of great extent off the north Irish coast, as off that of south Wales, is attested by the deeply submerged landscape off the Lancashire and Cheshire coasts, and by peat more than 50 ft. (15 m.) below sea-level in Heysham Harbour (Reid, 1913). Movius speaks freely of the land standing 120 ft. (36·5 m.) higher than at present, and to this phase attributes a facility for diffusion of cultures from Great Britain to Ireland. Nevertheless, he writes: 'Conditions similar to those of the present day resulted from the marine transgression of the *Atlantic* period.' Even if we follow Movius in the assumption he uses, and in his adoption of Jessen's correlations, we must conclude that the greater part of the transgression must have been accomplished before ever the Atlantic period began.

The *upper* lagoon sites at Cushendun are judged by their contained molluscan fossils to have accumulated near the low-water mark of a shallow tidal estuary: they formed near the top of the submergence, and it is fortunate that pollen analyses can be made in them. Indeed, by reference to similar deposits nearby Jessen is able to produce a short synthetic diagram (which we have also incorporated in Fig. 19), showing instructive trends in forest composition. Clear as these trends are, it is most difficult to relate them to our English scheme of forest history, still harder to refer them to the Scandinavian schemes, and not easy to compare them even with Irish diagrams. In the latter task Jessen has the advantage of reference to the large body of his unpublished Irish pollen diagrams, and his judgement must be respected. He says of the synthetic diagram for the lagoon deposits that it agrees very well with the upper part of zone V*b* in the pollen diagrams from Northern Ireland. However, the transition from Jessen's zone V to zone VI in Ireland is marked by the first substantial rise of *Alnus*, by very low minima of *Corylus*, and by a temporary maximum of *Pinus*. One would undoubtedly, on these criteria, tend to make Jessen's zone transition V–VI the equivalent of the English zone transition VI–VII, and in fact Mitchell specifically suggests correlating the English zone VI*c* with the Irish V–VI transition, which comes very nearly to the same thing. If this were so, we could go so far as to say that the full extent of the 25 ft. beach transgression had been reached within the English zone VI. Before, however, going so far as this, it would be well to extend comparison to the diagram (Fig. 20) from Newferry on the River Bann, where a clearly datable Neolithic industry was recovered from the extensive diatomite layers being dug commercially (Movius *et al.* 1936). The sequence of strata and the archaeological horizon are shown in Fig. 20, to which are added the levels of Jessen's Irish zones, following his own statements in the text (p. 256) of his later paper with Farrington (Jessen & Farrington, 1938). The end of zone VI is placed at the top of the diatomite layer through most of which the artefacts were found, and the transition from zone V to VI is in the lower peat, a short distance below the level where increasing wetness makes its record apparent in a change first to *Phragmites* peat and then to the nekron mud and diatomite of open water. Marine influence is not apparent in the diagram, and the site is so situated that sea-level change cannot be considered as responsible for the increasing depth of fresh water.

If we now attempt to refer the lagoon deposits diagram at Cushendun to some part of the Newferry section, we shall be forced to recognize that it agrees tolerably well with the lower half of the Newferry diagram. That is to say, the Cushendun *upper* lagoon deposits as shown by this correlation extend from the latter part of Irish zone V*b* to the middle of zone VI. Equally important is the fact that this correspondence demonstrates that the uppermost lagoon deposits, our best index to the highest reach of the submergence, were forming up to that period of Irish Neolithic culture which resembles the British Windmill Hill culture (generally now placed about 2500–2200 B.C. [Clark, 1940]). Jessen reports, without as yet giving pollen diagrams, that at two other sites close by, the register of marine ingression has been correlated with forest history. At Portrush, shore deposits of the transgression maximum overlie peat which falls into the Irish zone VI, and at Somerset, 2 km. south of Coleraine in the Bann Valley, marine transgression is shown by marine organisms intercalated in a brown mud layer, at the middle of the Irish zone VI (Jessen in Movius, 1940).

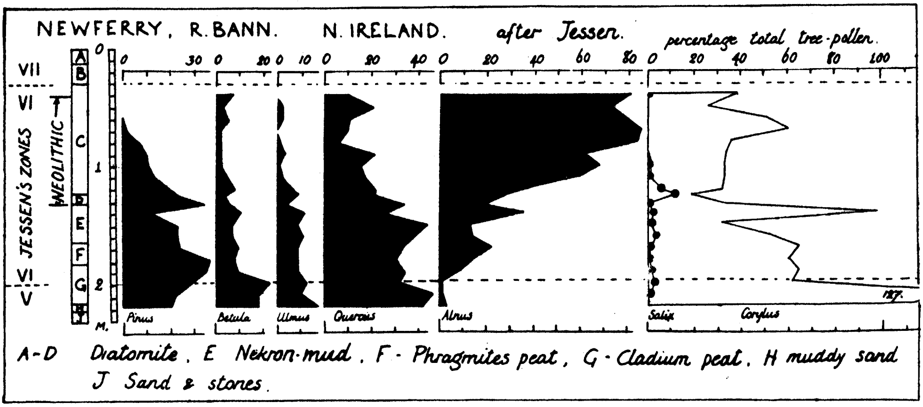

Fig. 20. Pollen diagram from Newferry, on the River Bann, Northern Ireland, after K. Jessen, showing correlation of Jessen's Irish zonation with the Neolithic culture found in the Bann diatomite.

From these data, based upon our acceptance of the correlation between Cushendun and Newferry, we should conclude of the marine transgression that it had already achieved the greater part of its extent in 'Boreal' times (English zone VI–Irish zone V*b*), and the remaining few feet of rise to the maximum for the raised beach occupied the time between then and the early Neolithic. If both the pollen horizon and the archaeological horizon are at all transferable from the Scandinavian region, this is a long period, of the order of 3000 years.

The raised-beach investigation at Glenarm has no polleniferous deposits, but the top of the beach predates a Neolithic culture in the overlying humus, and the occurrence of the northern *Cyprina islandica* in the beach gravels is taken to indicate cooler conditions after the climatic optimum. On the other hand, at Curran Point, the presence of the southern mollusc *Rissoa albella*, in thick estuarine clay beneath about 5 m. of beach deposits, confirms that the climatic optimum probably fell before the maximum marine transgression. Similar estuarine clay from Island Magee was referred by Jessen on pollen analytic grounds to the beginning of his zone VI, and from it instruments of Late Larnian type were recovered. An analysis published by Burchell from deposits beneath these estuarine clays, is hardly precise enough to be fitted into Jessen's zoning, though it may be noted that *Alnus* is present at a frequency similar to those of *Betula*, *Pinus*, *Ulmus* and *Quercus* (Burchell, 1934).

(v) *North Sea and east coast*

When we turn from the west to a consideration of the North Sea region, we encounter possibly the most interesting of all our submerged peats. This is the 'moorlog' which occurs extensively over the floor of the North Sea, especially in the region of the Dogger Bank. It is a hard, dark brown, fissile peat often brought up in quantity by the trawls of fishing vessels, and from material so obtained Mr and Mrs Clement Reid, with Whitehead & Goodchild (1909), have described the macroscopic plant content (see earlier). Pollen analyses were first published by Erdtman in 1924*b* and 1926, and his results, with others published later, are given in Table 1. It will be observed from what considerable depths these samples come: from 18 fathoms (108 ft. = 33 m.) to 29 fathoms (174 ft. = 53 m.) below the sea surface.

Samples 1–6 and 8–9 are remarkable in that they show pollen spectra in which pine and birch are completely dominant, the alder and other broad-leaved trees being unrepresented save for odd grains, and the hazel present in small amounts varying from 0 to 20%. Such composition can only refer to that part of the post-glacial sequence which we have put into zones IV and V. Sample 7 differs slightly from the others, in that it shows substantial amounts of oak pollen in two samples, and rather big percentages of hazel in all four. This would apparently indicate the opening stage of zone VI. Samples 7 and 8 are of particular interest because they were both dredged from between the Leman and Ower banks, some 25 miles from the Norfolk coast, where, somewhat earlier, the skipper of a steam drifter had dredged up from 19 to 20 fathoms a piece of peat containing a bone fish spear (harpoon) of Maglemose type. Analyses made by Jessen in the type sites in Denmark and by Thomson in Esthonia agreed in that they showed the culture to have occurred at the time of first expansion of the warmth-loving mixed-oak-forest trees: the Leman and Ower site might be supposed to be somewhat earlier (H. & M. E. Godwin, 1933).

Towards the present coasts of the North Sea, dredged-up peat samples of younger age have been described, and like sample 11 in the table, they often contain much *Alnus* pollen, though usually with abundant mixed-oak-forest tree pollen. Thus Lagerheim and von Post record pollen of alder, birch, hazel, pine, oak, lime, elm and sallow from material found off the Swedish west coast, and these trees are similarly represented in dredger samples from the estuaries of the German North Sea coast. To judge from the absence of later samples than zone VI*a* in the deep water of the North Sea, as well as from the absence of overlying clays in any thickness, we should suppose that the submergence of the North Sea took place in zone VI. As we shall see later, it also appears that the transgression reached almost its full extent during this period, so that here a rise of at least some 150 ft. (46 m.) in relative sea-level must have taken place. When we recollect

Table 1. *Pollen analyses of samples of moorlog from the North Sea*

No.	Long.	Lat.	Depth		Author	*Betula* (birch)	*Pinus* (pine)	*Alnus* (alder)	*Ulmus* (elm)	*Tilia* (lime)	*Quercus* (oak)	*Corylus* (hazel)
			Fathoms	Metres								
1	55° 10′ N.	4° 20′ E.	22	—	Erdtman	52	46	—	—	—	—	20
2	54° 50′ N.	4° 25′ E.	29	—	,,	2·5	97·5	—	—	—	—	1
3	55° 32′ N.	4° 27′ E.	18	—	,,	15	85	—	—	—	—	—
4	54° 50′ N.	4° 35′ E.	22	—	,,	—	100	—	—	—	—	—
5	54° 46′ N.	4° 0′ E.	28	—	,,	21	79	—	—	—	—	4
6	55° 0′ N.	4° 38′ E.	23	—	,,	16	84	—	—	—	—	8
7	53° 10′ N.	2° E.	19	—	,,	12	74	—	2	—	12	47
					,,	43	57	—	—	—	—	39
8	53° 10′ N.	2° E.	19	—	H. & M. E. Godwin	16	64	—	—	—	17	80 top
					,,	13	85	—	—	—	1·4	81 bottom
					,,	30	69	1	—	—	—	4
					,,	75	23	—	—	—	—	7
9	56° 25′ N.	5° 55′ E.	21	39	Vermeer-Louman	52	43	3	—	—	—	4·7
					,,	49	45	2	—	—	—	2
10	56° 25′ N.	5° 55′ E.	21	39	,,	27	73	—	—	—	—	1
					,,	38	59	2	—	1	—	19
					,,	8	92	—	—	—	—	5
					,,	6	94	—	—	—	—	8
11		Unknown			,,	4·3	95·7	—	—	—	—	9
					,,	3	27	68	—	—	1	—
12	Shore pebble (O. T. Jones)		Unknown		H. Godwin	39	40	—	16	—	5	184

the evidence from Somerset, Swansea, Northern Ireland, and the Scottish Lowland Plain, that there also a great marine transgression had been almost fully completed by the end of zone VI, the probability presents itself very strongly that this transgression must have been eustatic in character, following from a rise of sea-level all over the world.

It is clear that the fresh-water fen peats on the floor of the North Sea indicate that, before the submergence of zone VI, sea-level must have been at least 170 ft. (52 m.) lower than it now is. In order, however, to discover the duration and vertical extent of the marine transgression of this period, it is necessary to consider the evidence from the shallower waters of the North Sea coast, particularly such estuaries and bays as give promise of long records in their quiet-water deposits.

Clement Reid has drawn attention to the existence beneath the Humber of a post-glacial channel some 60 ft. deeper than the present river bed, and filled with 'silt and submerged forests'. The deposits of this region have not, unfortunately, been subjected to pollen-analytic investigation. Submerged forests on the Northumberland coast give only indefinite evidence of a small transgression later than zone VI, and the same may be said of the site at Skipsea Withow on the Yorkshire coast, where erosion has now exposed on the beach the lowest layers of a fresh-water lake. In these layers, which belong to zone VI*c*, there occurred not only remains of elk, reindeer, and a fresh-water *Ancylus* fauna, but in all probability another Maglemose fish spear of the type already mentioned as found between the Leman and Ower banks. Marine deposits do not, however, enter the deep profile of deposits succeeding these basal layers.

South of the Humber lies the great shallow estuary of the Fenland basin, of which an extensive account has already been given (Godwin & Clifford, 1938; and Godwin, 1940*a*).

Long lines of borings have made it clear that the relationships of the post-glacial deposits are, broadly speaking, those illustrated in the schematic Fig. 21. Deep glacial or late-glacial channels in the floor of the Fenland contain peats of zones IV, V and VI, as is shown in the diagrams from Old Decoy (Fig. 22) and Wilton Bridge. Peat formation in these zones is restricted to such channels, but in zone VII has become widespread, although whether in consequence of a changed climate, or of waterlogging due to rising sea-level, is not clear. During late Neolithic times, i.e. in the second part of zone VII, there took place the most extensive marine transgression in the Fenland history, during which the 'fen clay' was laid down as far inland as Ely. At this time very extensive shallow lagoons of brackish water reached almost the full extent of the present Fenland basin. In the period which followed peat formation continued, pine- and birch-woods grew above the fen clay, and peat formed far seawards, whilst Bronze Age man occupied the dry peat surfaces nearer to the Fen margin. These peats are referred to the end of zone VII, and to the transition zone VII–VIII. In the succeeding Romano-British period there was laid down upon the surface of the upper peat the thick belt of silt which forms the fertile 'Marshland' surrounding the Wash, and extends as tapering banks or 'roddons' along the natural river courses into the peat land behind the coastal bank of silt. Within the silts themselves and densely upon their surface are the traces of Romano-British occupation, so that in time of formation they appear to correspond exactly with the coastal clays of the Somerset Levels. In their configuration also the two deposits are closely similar, both undoubtedly corresponding with the 'Hochland' of the German north-west coast, as the peat lands behind correspond with the north-west German 'Sietland'. This upper silt must fall within zone VIII, but peat of this and later stages is

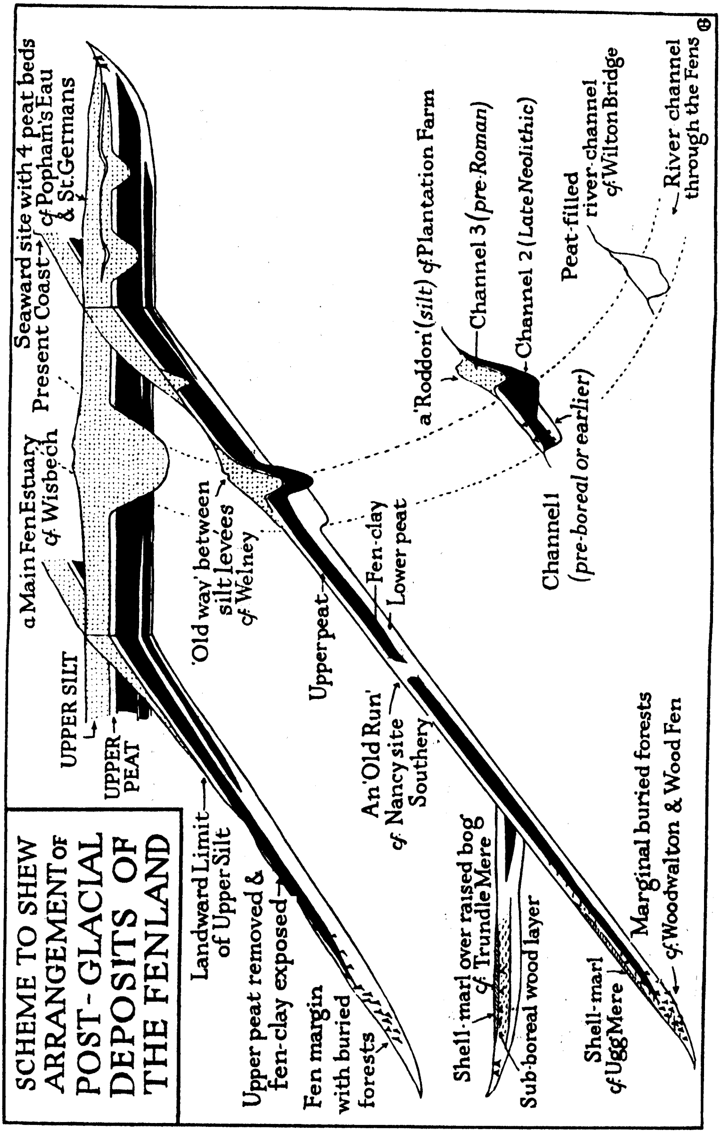
SCHEME TO SHEW ARRANGEMENT OF POST-GLACIAL DEPOSITS OF THE FENLAND
UPPER SILT
UPPER PEAT
a Main Fen Estuary of Wisbech
Seaward site with 4 peat beds of Popham's Eau & St. Germans
Present Coast
Landward Limit of Upper Silt
Upper peat removed & fen-clay exposed
Fen margin with buried forests
'Old way' between silt levées of Welney
Upper peat
Fen-clay
Lower peat
An 'Old Run' of Nancy site Southery
a 'Roddon' (silt) of Plantation Farm
Channel 3 (pre-Roman)
Channel 2 (Late Neolithic)
Channel 1 (pre-boreal or earlier)
Peat-filled river-channel of Wilton Bridge
River channel through the Fens
Shell-marl over raised bog of Trundle Mere
Sub-boreal wood layer
Shell-marl of Ugg Mere
Marginal buried forests of Woodwalton & Wood Fen

Fig. 21. Purely diagrammatic scheme to show the general lines only on which post-glacial Fenland deposits are arranged. (Reproduced from *Scientific Survey of the Cambridge District*, ed. H. C. Darby.)

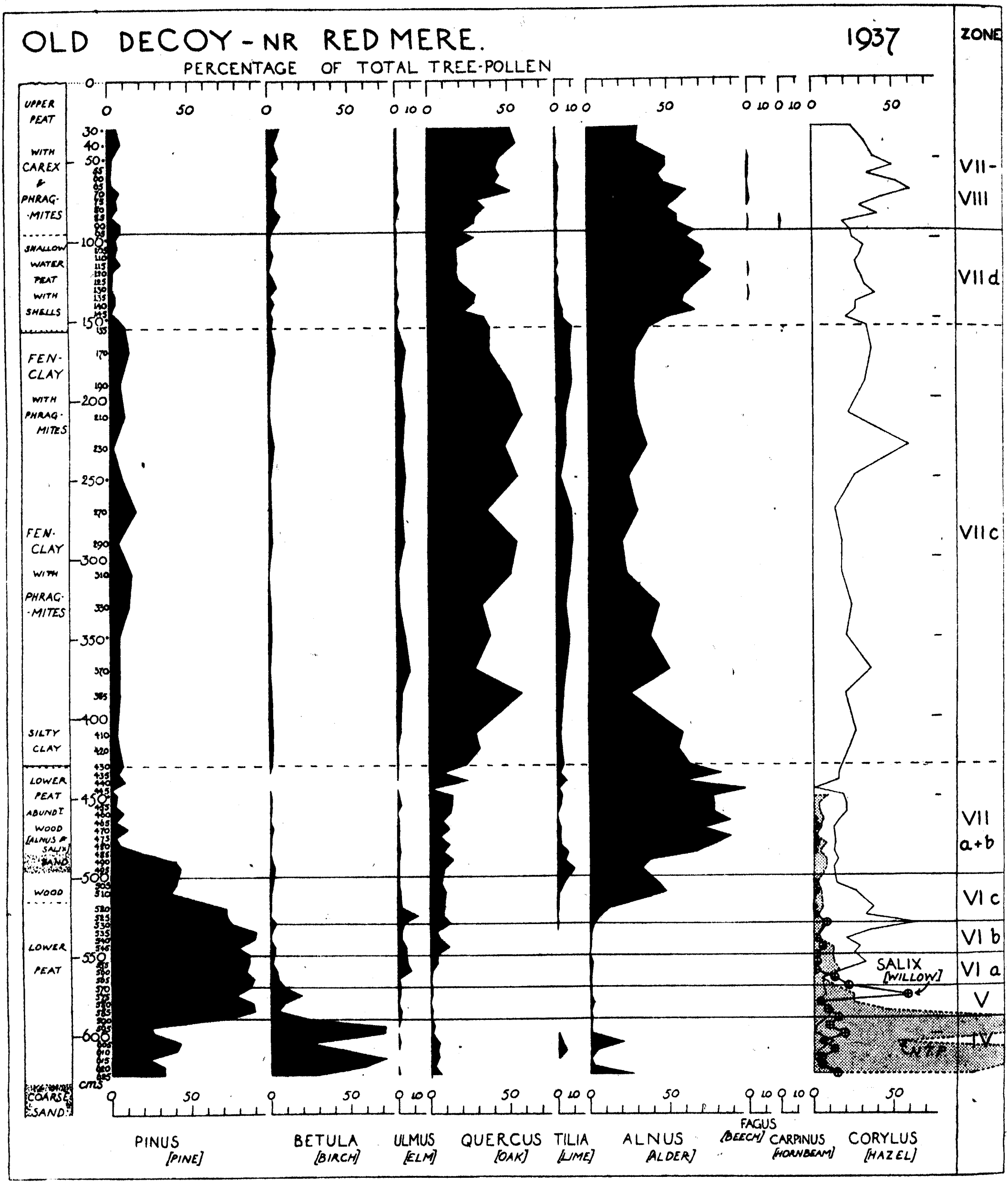

Fig. 22. Pollen diagram from Old Decoy, in the natural valley of the River Little Ouse, near Shippea Hill, Cambridgeshire. The fen clay represents the extreme landward penetration of the most extensive post-glacial marine transgression in the Fenland. (Reproduced from *Philos. Trans.*)

almost completely lacking. It is possible that the many shallow meres of the undrained Fenland, Whittlesea, Benwick, Soham, and Ugg, meres had their origin in this zone and may indeed have been caused by the backing up of fresh water during the submergence.

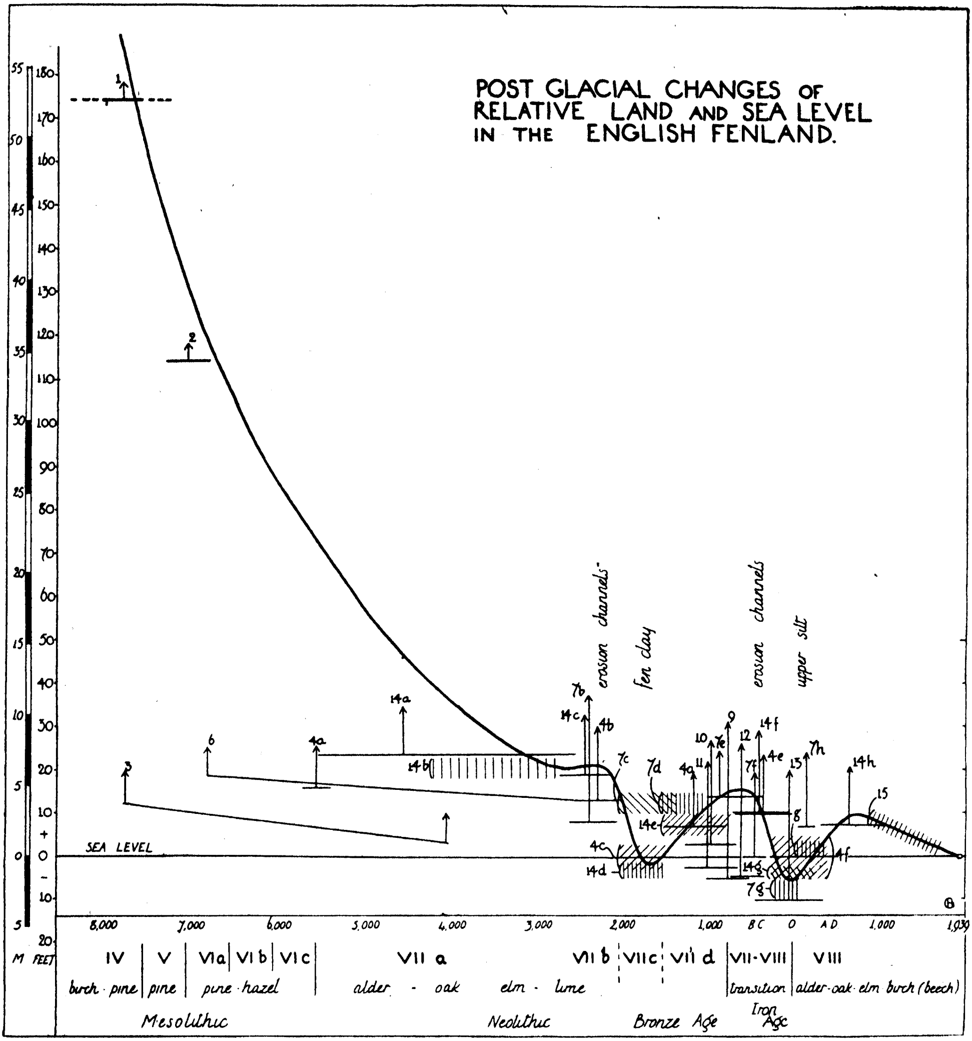

Fig. 23. Curve representing relation of land-level to sea-level in the Fenland throughout the period shown on the base-line. The convention of constant sea-level has been used. The numbered lines and shading represent the indices from which the curve was constructed. (Reproduced from *Philos. Trans.*)

The results of the Fenland investigations in their bearing upon the former relative position of land and sea have been summarized in the diagram of Fig. 23, from which it will be apparent that we recognize a long history of marine transgression, extensive and rapid in zones V, VI and early VII, but later slower and interrupted by stages of regression, the first in the middle of zone VII when the wood peats of Neolithic times grew over the fens, the second at the end of zone VII and in zone VII–VIII, when peat spread out over the fen clay and Bronze Age man occupied the peat lands, and the last after the Romano-British transgression. Incomplete as this diagram clearly is, it nevertheless indicates a technique for applying the pollen-analysis chronology to problems of change in sea- and land-level.

We may next ask how this disposition of fen deposits, described above in its simplest outline only, is reflected in the formation of coastal peat beds. To begin with we may note that samples from the deeper river channels near the Wash have not been recovered, and thus peats of zones IV, V and VI are not represented, although possibly 'moorlog' from the Lynn Deep would turn out to be of this age. The deepest exposures of coastal peats are those already referred to at St Germans, near King's Lynn, where the thin bottom peat rests on Kimmeridge Clay 23·5 ft. (7·2 m.) below mean sea-level. The pollen content of this bed shows it to belong to zone VII, and it therefore follows that at the end of zone VI, sea-level on this coast must have been at least 23·5 ft. (7·2 m.) lower than at present. Now in Somerset at this time we have seen that sea-level must have been about 5 or 6 ft. (1·5 or 1·8 m.) *above* present sea-level. Thus since the end of zone VI it becomes apparent that there must have been a downward tilting of the east relative to the west coast of the order of at least 30 ft. Of the great transgression in zone VI itself there is not much evidence in the Fenland, for this later differential warping would itself suffice to explain the present depths of the channel peats of zones IV, V and VI. However, we can be satisfied that it occurred, for the peats between the Leman and Ower banks already mentioned lie very close to the entrance to the Wash.

Taken together with the fact that considerable east-to-west warping has occurred since zone VI, we may note that whereas in the west, in Somerset and Borth particularly, there was evidence throughout the long period of zone VII of freedom from any extensive marine transgression, in the Fenlands, on the contrary, in the middle of this zone there occurred the most extensive phase of marine transgression. Nor can this dating possibly be due to error in pollen zoning, for whereas at Shippea Hill in the Fenland the fen clay lies between a Neolithic and an Early Bronze Age horizon, in the raised bogs of Somerset the uninterrupted raised-bog peat continues between the Neolithic, Iron Age, and Romano-British occupation levels. Thus, although the fen clay does not necessarily indicate a very considerable rise in relative sea-level, it seems likely that it is connected with the east-west warping of the country and is therefore primarily due to isostatic, and not to eustatic change in sea-level.

In the excavations at St Germans four peat beds were encountered, and it must be admitted that their pollen analyses served very little towards a direct dating. Nevertheless, taken with thickness, level, and the character of the intervening clays, their appropriate zoning was fairly clear. The thin tree layer (C) lying at about −17 ft. O.D. belongs to zone VII and corresponds to the lower peat farther inland. The 2 ft. peat bed (E) at −3 to −5 ft. (0·9–1·5 m.) O.D., which yielded such complete evidence of vegetational succession (see p. 201), belongs to zone VII–VIII, a reference according with the alleged discovery in its surface layers of glass beads which archaeologists said might be of any age from La Tène to Anglo-Saxon. The uppermost peat is thin and not widely represented in the Fenland; it will be noted that beech is present in its pollen diagram.

Wherever borings are made near the coast of the Wash they reveal the equivalent of the 2 ft. peat bed, and on the flanks of the Wash at Ingoldmells on the Lincolnshire coast it is represented by the upper of the two peat beds on the shore (Swinnerton, 1931). This thin upper peat contains a Halstatt salt-making industry, and is succeeded by 'Scrobicularia clays' which, it has been suggested, post-date the occupation of an adjacent Roman site. The lower shore peat at Ingoldmells is rooted in boulder clay and is referable to zone VII, corresponding to the top of the lower peat in the landward Fens, whilst the overlying Triglochin Clays correspond to the fen clay. Vaguely determinable 'Neolithic' artefacts have been found in this lower peat.

The persistence of the upper peat seawards over the fen clay and its considerable thickness argue a period of freedom from marine influence in the last part of zone VII and in zone VII–VIII. In zone VIII, however, fell the deposition of the marshland silts, and since these correspond in date so closely with the clay belt of the Somerset Levels, it is possible that here once more we are dealing with a eustatic rise in sea-level. Although a suitably late transgression is recorded from Borth also (p. 225), it will need recognition at widespread sites before this contention is proved.

Along the East Anglian coasts from the Wash to the Thames Estuary there occur many exposures of coastal peats, and peat pebbles are frequent upon some of the shingle beaches (Table 1). Between Hunstanton and Holme-next-the-Sea, a peat bed is disclosed from time to time on the foreshore, and from this R. A. Smith has reported the discovery of a flint celt of the 'Dolmen period'. The pollen content of the peat was *Pi* 3 %, *Be* 2 %, *Ul* 0, *Q* 12 %, *T* 10 %, *Al* 73 %, *Co* 7 %, and this suggests that the bed corresponds with the lower peat at Ingoldmells.

A little farther west, at Brancaster near Scolt Head Island, several peat beds occur at different levels. The surface of the deepest peat is seen at Judy Hard in Brancaster Harbour at ebb tide, and borings show it to be 8·5 ft. (2·6 m.) thick. It yields a very interesting pollen diagram, in which zones IV, V, VI and part of zone VII are readily recognizable (Godwin, 1940*a*). Since the top of the bed now lies at −1·5 ft. (0·45 m.) O.D., we can take it that this evidence indicates that although net submergence must have gone on to bring the peat to its present level, the sea did not reach its present level until a good way into zone VII. This indicates that our deepest Fenland peats at St Germans are not likely to belong to the *early* part of zone VII.

On the harbour channel foreshore and also outside the harbour thin peat beds occur at levels between −2·5 ft. (0·75 m.) and −5·5 ft. (1·7 m.) O.D. (Table 2). Analyses of these beds is difficult, and the sparse grains do not allow any close correlation (Godwin, H. & M. E. 1934).

Farther still along the Norfolk coast we fringe the territory of the Norfolk Broads, a district of great importance to inquiries such as we are now considering. This area represents, like the Fenland, a valley system drowned and waterlogged by marine transgression, but it has suffered much less interference by human drainage activity, and on that account preserves not only topographical features now absent from the Fens, but keeps in relatively unaltered condition the natural hydrosere communities which formerly must also have covered our Fenlands. As we have learned to expect, we find that in the seaward ends of these valleys the alluvium is marine in origin, whilst the landward part is peat. Apart from the tidal stretches of Breydon Water and Oulton Broad, the Norfolk Broads are shallow, fresh-water, open lakes in the peat land, and they would appear to correspond in position with the now drained meres of the Fenland. Extremely promising

Table 2. *Pollen analyses of coastal peats in south-east England (percentage total tree pollen)*

Site	Author	No. of tree pollen Depth in.	No. of tree pollen Counted	*Pinus*	*Betula*	*Ulmus*	*Quercus*	*Tilia*	*Alnus*	*Fagus*	*Carpinus*	*Corylus*
Shore peat, Hunstanton	H. & M. E. Godwin	—	150	3	2	0	12	10	73	0	0	7
Brancaster Channel	„	—	31	13	0	0	23	0	64	0	0	32
		—	115	17	4	0	63	0	25	0	0	14
Brancaster Golf Club	„	19	40	10	10	0	27	0	52	0	0	82
		5	55	15	4	0	29	2	40	11	0	46
		1	40	15	0	2	55	2	25	0	0	57
Lion-Point, Clacton (grooved-ware site)	„	8·5	50	18	2	2	64	2	12	0	0	20
		6·5	50	10	4	0	64	4	18	+	0	32
		3·5	50	6	0	0	64	16	12	2	0	34
		1·2	50	14	2	0	64	8	12	0	0	30
			(Not percentaged)									
Stone-Point, Walton	„	4·5	10	2	0	0	7	1	0	0	0	1
		2·3	20	0	0	1	10	0	9	0	0	20
		0·5	20	0	1	0	13	0	6	0	0	14
Hullbridge-on-Crouch:												
Upper-peat	„	—	50	4	16	0	56	2	22	0	0	40
Lower peat (late mesolithic)	„	12	150	2	1	+	63	7	5	+	+	37
		11	150	3	2	2	78	5	9	0	0	54
		10	150	1	0	0	81	9	8	0	0	26
		9	150	+	+	7	75	7	9	0	0	34
		8	150	+	2	3	76	7	11	+	0	25
		7	100	8	1	3	50	26	12	0	0	21
Lower Halstow (Burchell)	Erdtman	Clay		2·5	7·5	5·5	61	14·5	9	0	0	
		Peat		1	4	+	89	2	3	0	0	

preliminary field work has been carried out by Mr J. S. Jennings in the valley of the Ant, and in relation to the profiles he has made, a number of pollen analyses series have also been examined. We will not anticipate the completion and publication of this work except by illustrating a single pollen diagram from the deposits in Barton Broad (Fig. 24). Jennings has shown that wood peat underlies the whole extent of the Broad beneath the

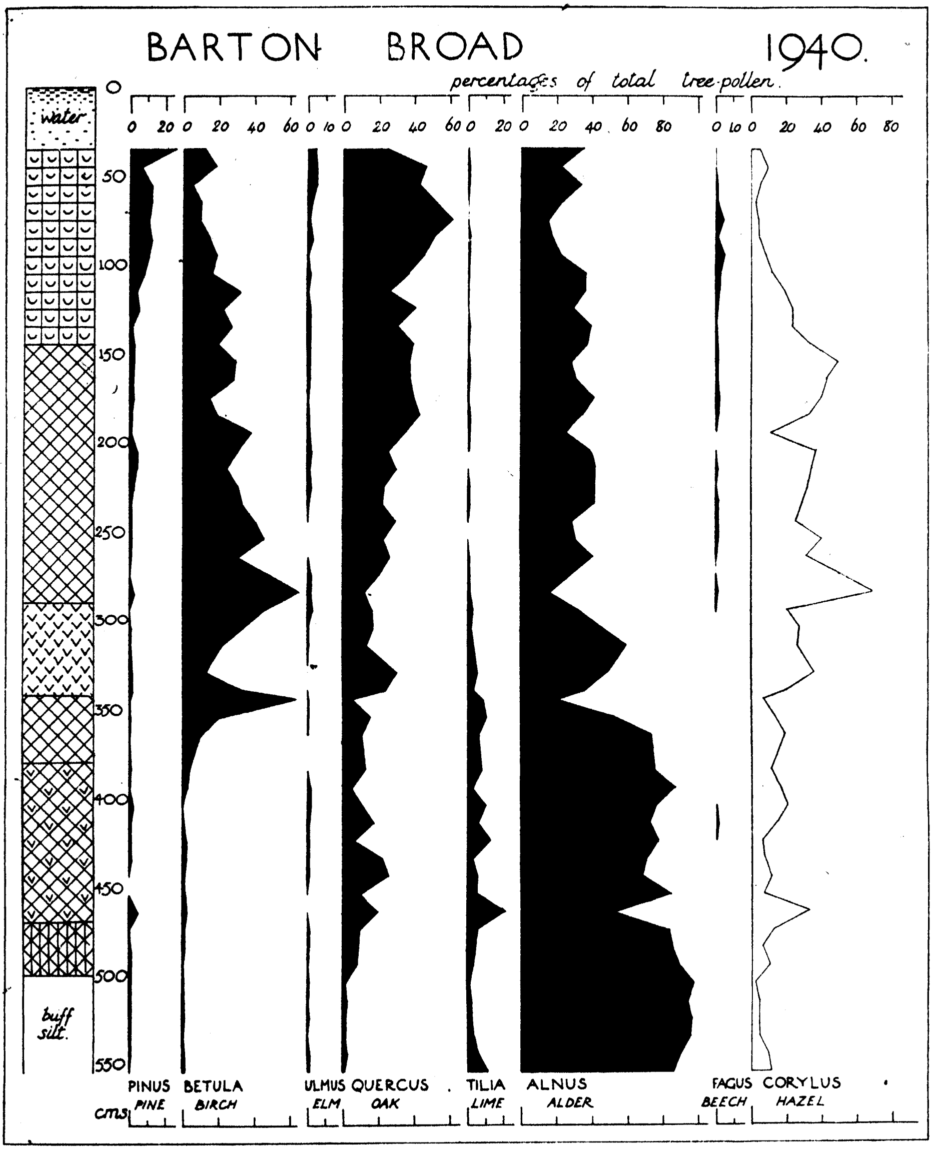

Fig. 24. Pollen diagram from Barton Broad, Norfolk, from samples collected by J. S. Jennings. The top 250 cm. or organic lake-muds overlie wood-peat (*v*—symbol) and woody detritus mud.

true lake muds. The pollen diagram indicates that the transition from the one type of deposit to the other occurs at a well-defined horizon. The considerable rise of *Betula*, the decrease of *Tilia*, the appearance and consistent small representation of *Fagus*, all indicate that this horizon is the opening of zone VIII. It is thus apparent that this Broad (and probably the others) has a very recent origin, just as the Fen meres were shown to have. As for the Fenland meres, we may inquire whether the Roman marine transgression was responsible for their formation, or whether it is to be attributed to the so-called 'sub-Atlantic climatic degeneration'. From the fact that these Broads are at present in direct river communication with the sea, and that their water-level is but a foot or two above sea-level, we may see that a rise of the sea to its present level would almost certainly have brought such Broads into existence (had they not previously existed) by the backing up of fresh water in the drowned valleys. This problem, together with the whole question of correlation with Fenland stratigraphy and history, is of the greatest interest, and warrants thorough investigation of the Broads region.

The section of coastline southwards from Yarmouth up to, and including, the Thames estuary, is one long famous for its submerged land surfaces, and, particularly along the Essex coast, the patient researches of Hazeldine Warren and others (1936) have established the existence of what has been called a 'Lyonesse occupation surface', now exposed between tide marks. It has been shown in the neighbourhood of Clacton that this surface, which rests upon pre-Quaternary rocks, and slopes seawards down the beach, gives evidence of continuous occupation from late Mesolithic to Early Bronze Age times. Nothing later than 'B' Beaker is, however, found upon it. The artefacts are below and within a thin peat layer which is overlaid by a scrobicularia clay, which we may take as indicating the phase of submergence by which the long period of occupation was brought to a close. We may recall that the great transgression in the Fenland which deposited the fen clay had an 'A' Beaker horizon just above it, so that unless the 'B' Beaker is older than 'A', we cannot assume the two submergences to be of the same date. As might perhaps be expected, the pollen analyses of the thin peat bed are not very instructive. The peats are silty, contain remains of saltmarsh plants, and very high percentages of pollen of Chenopodiaceae type. Tree pollen is very sparse, as can be seen from the results in Table 2. The rather high *Tilia* and sparse *Fagus* are of interest, since in the Fenland they are together found in the Bronze Age peats just over the fen clay.

Still farther south, at Hullbridge on the River Crouch, Reader and Hazeldine Warren described two beds of peat exposed by tidal scour in the estuary and covered and separated from one another by silt. Beneath the lower of the two beds is a complete and pure flint industry described by Clark (1932) as belonging to the late Mesolithic culture. This late Mesolithic dating is confirmed by the pollen analyses (see Table 2), for alder and the mixed-oak-forest trees are completely dominant. The prevalence of *Tilia* suggests that the peat belongs to zone VII, though this is somewhat early for the scattered *Fagus* and *Carpinus* grains. Analysis of the upper peat unfortunately gives little information as to age.

The elaborate dock excavations in the Thames estuary have produced a wealth of sections in the alluvium, and in places such as Tilbury Docks, as many as three buried peat beds have been disclosed. In some of these beds long ago Pepys remarked the ancient yews and oaks now well below sea-level. It is true that Romano-British surfaces appear at levels well within present tidal range, but it is uncertain whether they reached this position as a result of compaction of the alluvium below them or because of change in relative land- and sea-level. It is unfortunate that there has been almost no opportunity to make pollen analyses of these beds, and their dating by archaeological means is scanty. However, a beginning in this direction has been made in the investigations of Burchell (1928) at Lower Halstow in the Medway, north Kent. The following is Burchell's composite section:

		ft.	in.
1.	Humus	1	6
2.	Blue marsh clay	1	6
3.	Rusty marsh clay		7
4.	Peaty clay		2
5.	Rusty marsh clay with race		6
6.	Early Iron Age land surface		1
7.	Grey marsh clay with twigs	2	0
8.	Brown marsh clay		6
9.	Peat	2	0
10.	Epipalaeolithic factory site		2
11.	Gravel of 10 terrace	3	0
12.	Marsh clay		
13.	London clay		

It is interesting to learn that in analysis from the post-Early Iron Age layer no. 4, Erdtman found pollen of *Fagus*. Samples from the peat and clay overlying the flint industry are shown in Table 2, and it seems probable that they both belong to zone VII. This would indicate that the culture must correspond with the latest part of the Mesolithic, and this conclusion is accepted by Clark, who, in comparing the Lower Halstow flint industry with that of Ertebølle in Denmark, says that in general the two have much in common, though in detail they diverge greatly.

It must be apparent that rich as is the south-east coast in opportunities for gauging land- and sea-level movement by correlation of alluvial stratigraphy, pollen analysis and archaeology, these chances remain untaken. It can only be said that the evidence we now have does not contradict nor indeed much supplement that from the Fenland Basin.

CONCLUSIONS

The main conclusions of this survey of coastal peats round the British Isles may be summarized as follows:

(1) Submerged peats represent short and local successions of vegetation such as are now evident round European coasts, and may supply some information of the ultimate stages of successions which are no longer easily available from existing vegetation, disturbed as it is by human interference.

(2) Submerged peats may be shown by pollen analysis to have formed at all stages of the late-glacial or post-glacial period, and although perhaps more frequently at some times than others, it is clear that not the slightest justification remains for using the concept of a 'submerged forest period', still less the 'Neolithic submerged forest period': the concepts are obsolete and should be discarded.

(3) Study of submerged peats datable by pollen analysis establishes the fact that the great period of post-glacial eustatic rise in sea-level occurred at the time of first expansion of warmth-loving trees. The depth of the moorlog from the Dogger Bank region is so great that if we agree it was chiefly submerged by eustatic rise in sea-level, then this rise (at least 170 ft. [52 m.]) accounts for a very large part of the *total* eustatic rise to be expected during the post-glacial period upon the average of recent calculations. That is to say, that at the time the deepest North Sea peat was forming very little recession of the ice can have gone on in Europe, and the peats must on this account alone be considered as late

glacial or very early post-glacial. This agrees with our reference of them to pollen zones IV or V, and with the fact that the last 50 ft. (15 m.) or so of the big eustatic rise took place within zone VI of our schema for England and Wales. This transgression caused the formation of the North Sea to almost its present extent, and made the effective separation of the British Isles from the European mainland.

(4) The last stages of this great transgression were responsible for the formation of the 25 ft. raised beach in the north of Ireland and in Scotland, and only the last few feet of the rise in relative sea-level extended into zone VII. Marine deposits of the end of zone VI indicate a pronounced 'post-glacial warmth maximum'.

(5) The present situation of the 25 ft. raised beach gives evidence that since its formation these islands have undergone considerable tilting from north to south. Our results add that during the same period the east has tilted downwards relative to the west.

(6) There is some indication that there may have been a eustatic rise in sea-level during Romano-British times. Since this time there is no evidence of net east to west tilting.

(7) We have deliberately avoided writing of the '*Littorina*' transgression, and have intentionally not referred to the 25 ft. beach as the '*Littorina*' beach. Such usages can only justifiably be made after judicial estimate of the evidence for correlating the British and Scandinavian phenomena of land- and sea-level change.

In conclusion I take this opportunity to thank the Royal Society of London for the loan of boring apparatus, and for generous financial aid, which facilitated many parts of the author's own contribution to the coastal pollen analytic and stratigraphic investigations referred to in this paper.

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REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 12, No. 1, May 1943

This number is printed in small type in order that the continued output of ecological work may not remain unpublished through wartime cuts in paper supply. There are five original papers, six reviews and ninety-seven Notices of Publications on the Animal Ecology of the British Isles. R. Bassindale contributes No. 11 in a comprehensive series on the biology of the Bristol Channel, comparing the varying salinity conditions of the Tees and Severn estuaries. An estuarine animal has to adapt itself not only to the different salinities with each day's high and low water or with spring and neap tides, but also to the varying rates of change of salinity. Conditions alter with distance from the mouth and are most severe about half way up both estuaries. The quantitative distribution of intertidal fauna on the Northumberland coast was studied by F. Brady. He found a definite zoning of the regions of maximum abundance of the commoner species, largely depending on the differing amounts of exposure between tides at various levels up the beach. No correlation was found with salinity.

In the Hope Department of Entomology at Oxford, C. B. Lewis and J. D. Bletchley studied the emergence rhythm of the dung fly, *Scopeuma stercoraria*. A rhythm of emergence in the daytime appears to be inherited; for in constant light or darkness the rhythm continued, though less pronouncedly. L. S. V. Venables, at Binsey, near Oxford, counted the emergence of pipistrelle bats from the church roof each evening (346 were seen once). Greatest numbers came out in May to August: at about sunset in August, but after sunset at other times of the main season.

An important contribution to animal population work is the joint paper by R. A. Fisher, C. B. Williams and A. Steven Corbet. Based particularly on the latter's collections of Malayan butterflies and on Dr Williams's catches in a light-trap at Rothamsted, Dr Fisher provides a mathematical formula for the relation between the size of a sample and the number of species in it. The latter increases by 'α'—the index of diversity—for each increase of e (2·718) in the size of the sample. Thus in a population where $\alpha = 14$, 60 species would be produced by a sample of 1000 individuals; but only ten more species would be added if the sample were doubled.

Reviews cover the *Journal of Ecology*, the first annual report of the Indian Ecological Society, the problem of the depletion of sea-fish, 'Bird display', 'The birds of Britain', and two reports on bed-bug investigations.

Dennis Chitty

Robinson, Sir Roy. Some ecological aspects of afforestation and forestry in Britain. *Forestry*, **16**, 1, 1942.

This article is of value as a summary of the experience gained in the afforestation of difficult sites in Britain. In addition, two working hypotheses of great ecological interest are put forward as a result of this practical experience. The hypotheses are as follows:

1. *Accelerated succession.* In the natural afforestation of difficult sites some species are pioneers and some are successors. It is not feasible by artificial means to bring in the successors in advance of the pioneers. It is possible, however, to accelerate the natural succession by mixed planting of pioneers and successors and by appropriate thinning treatment to complete the succession in the course of a single rotation. A successor on one site may be a pioneer on another.

2. *The silvicultural stream.* In the silvicultural treatment of woodlands, the most effective methods are those which proceed in the direction of a natural succession of vegetation.

The hypothesis of accelerated succession is based on the following facts. On certain difficult sites, particularly those under heather, species such as Douglas Fir, Norway Spruce and occasionally Sitka Spruce, may fail to develop if planted in pure stand. On the other hand, if these species are mixed with Scots Pine, the latter may grow freely at first, to be followed by the Douglas Fir or spruce, which has then frequently tended to outgrow the pine and, according to such evidence as is now available, may ultimately suppress it. There is thus evidence that Scots Pine can act as a pioneer species. Other species which appear to be similar include Corsican, Austrian and Mountain Pines, and also Birch, European and Japanese Larch, though the latter three species have been less frequently used in this way. In contrast, *Tsuga heterophylla* appears to resemble the spruces and Douglas Fir in being a successor species.

At the other extreme of the difficult sites are some open chalk downs. The evidence available is that pure beech and pure ash plantations check on these sites almost as badly as do spruce plantations on *Calluna* sites. On the downs, however, Scots, Corsican and Austrian Pines play the same part in bringing on beech and chalk ash as they do with spruce on heather. Curiously enough, there is some evidence that Norway Spruce will also serve the same purpose as pine in acting as a pioneer species on chalk.

The question arises as to what may be the effect produced by the pioneer species. It is suggested that the pioneer species in some way prepares the soil for the growth of the successor species, which presumably has more exacting requirements. From time to time, various tentative suggestions have been made which subsequent experience has hardly borne out. For example, it was observed that sites with short heather were often difficult even for pines, but that if the heather had been allowed to grow long, there was a marked improvement in the value of the site for planting purposes. It appears possible that long heather tends to aerate the soil, for the roots run well down and may occasionally be traced through an iron pan. There is possibly also some increase in the phosphatic content of the soil, and it is found that Sitka Spruce when planted pure does far better on long than on short heather.

In many cases where spruce in pure stand (planted with vertical notching) had remained in check, at times for as much as 20 years, examination of the individual plants showed that the deepest roots had died and that the plants had had to form new and very long superficial root systems before they could begin to make appreciable height growth. It was concluded, therefore, that soil aeration was very important, and from such facts as those cited was developed the well-known system of turf planting. This worked excellently on grassy sites, where it has become the standard practice, but it did not prove successful on heather sites. Next there was developed the system of deep ploughing with caterpillars and heavy ploughs, which, while giving improved results in planting spruce on heather sites, still falls short of expectations. The present method is to plough deeply first and then to plant mixures of species such as pine and spruce, with results of the type already discussed.

The author suggests that the development of pioneer species in the cases studied is associated with self-propagating soil changes, possibly fungal in origin and possibly of a similar kind to the beneficial action of composts recorded by Rayner, which was also self-propagating among pines. It is recognized that improvements are most noticeable when growth of the trees has been sufficient to form a complete canopy. Striking increments in shoot growth may follow this stage. It would seem (to the reviewer) that this implies that the bar to effective tree growth may often be associated with the micro-climate and perhaps particularly with lack of shelter effects.

The general attitude adopted in this paper is clearly in harmony with our ideas on woodland succession —although it might possibly prove profitable to develop more fully the contrasts between primary and secondary successions, for planted woodlands differ clearly from primary successions in that the soil has already developed fully in the biological sense. Indeed, in this paper, many of the difficult sites are referred to as on 'much degraded soils' and this is clearly the logical way of regarding those of heathy origin. For the rest, two notable assumptions are implied in these pages. One of these is the failure of the traditional 'agricultural' or 'fertiliser' method of looking at soils, a failure which almost all ecological experience endorses. Equally noteworthy is the implication that the effects of clear felling may be devastating as far as soil conditions are concerned, and this also is in agreement with ecological expectations.

W. H. P.

John Ray, Naturalist. By **C. E. Raven.** Pp. 502 + xx, 1 plate. Cambridge University Press. 30*s.* net.

Although this book is in no sense ecological, the importance of Ray's work to biology is so great that no apology is needed in drawing attention to it, especially as it is a remarkable fact that no adequate biography of John Ray has previously appeared. It has been left to Dr Chas. E. Raven, Master of Christ's College and Professor of Divinity at Cambridge, to fill the gap and to do it in a form which is full, sympathetic and authoritative. It may be doubted whether any professional biologist of to-day could have done equal justice to the subject. But Dr Raven, like Ray, is a scholar, a divine and an all-round field naturalist. In addition, his writings show that he has long been interested in and has studied deeply the history of thought in England and particularly the development of scientific thought. The combination of these qualities has raised a book which in any case would have been a valuable biographical record, to a real distinction.

There is great interest in the record of Ray's journeys and discoveries, and, perhaps particularly, because many of the localities he mentions are evidently still in a state comparable to that in which he saw them and are often still occupied by the rare species he first recorded. Later comes an account of the manner in which Ray gradually embarked on the labour of publication and finally on the writing of his fullest and largest works. The scope of these is tremendous. Ray is shown as a founder of systematic biology with a detailed knowledge of plants and animals which was remarkable in its accuracy and completeness. He had a gift for the analysis of taxonomic relations which has been equalled by few and exceeded by none. His industry must have been enormous and the range of his knowledge is as remarkable as the mastery he displays over its details.

Ray, however, occupies an outstanding place in the development of scientific thought in another respect. On the biological side, he represents a development of the Baconian revolt against the formalism of the schools and the narrow limitation of academic studies. From this point of view he occupies, although in a widely different direction, a position almost Newtonian in its prominence and in the catholicity of its interests.

This is a book which every biologist should read as well as a notable contribution to the history of science.

W. H. P.

ERRATA

The Mycorrhizal Relations of Pinus

Two sentences referring to *Mycelium radicis nigrostrigosum* on p. 42 of this volume should be transferred to the bottom of p. 41. This form is not pseudo-mycorrhizal.

RUSSIAN-ENGLISH TECHNICAL GLOSSARIES

Owing to the shortage of comprehensive Russian-English scientific and technical dictionaries, at the request of the Anglo-Soviet Scientific Collaboration Sub-Committee, a number of Russian-English glossaries has been collected and housed in the Science Library, South Kensington, where they can be consulted.

1. Glossary of Russian Names on Maps.
2. English-Russian and Russian-English Technical, Military and Naval Dictionary (Vickers Ltd., 1918).
3. Russian-English Glossary (Metallurgical Terms).
4. Glossary of Russian Medical Terms.
5. Telecommunication Vocabulary in eight languages.
6. Russian-English Index to Drawing of Steamers.
7. Russian List of Birds.
8. Naval Equivalents (2 volumes), 1924. Prepared by the Naval Staff, English Division, Admiralty.
9. Dictionary of Russian Naval Equivalents (1 volume), 1934. Prepared by the Naval Staff, English Division, Admiralty.
10. Russian-English Technical Glossary, dealing mainly with Fuel Technology, by R. A. Acton Taylor, Fuel Research Station, S.E. 10.
11. List of Russian Words and Phrases dealing chiefly with the Bacteriology of Fish, by Dr James M. Shewan.
12. Russian Botanical Terms, by Kenneth Airy Shaw and P. A. Dattan.
13. Glossary of Common Names of Plant Diseases.
14. Glossary of Botanical Terms.
15. Technical Glossary by Harold Oatfield.
16. Technical Glossary by Dr Julian F. Smith.
17. List of Abbreviations commonly used in the U.S.S.R., by G. Z. Patrick (Department of Slavic Languages, University of California). Revised edition (1937). In co-operation with American Council, Institute of Pacific Relations, 129 East 52nd St., New York.
18. Russian-English Glossary of Terms used in Animal Ecology.
19. Comparative Ukrainian/Great Russian/English Glossary comprising a brief Ukrainian Grammar.
20. Russian-English Glossary (Medical).

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BY

W. H. PEARSALL

VOLUME 32
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WITH FOUR PLATES, AND NUMEROUS
FIGURES IN THE TEXT

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CONTENTS

PAGE

ORIGINAL PAPERS

E. G. Davies. Figyn Blaen Brefi: a Welsh Upland Bog. (With Plate 1 and eight Figures in the Text) 147

E. Price Evans. Cader Idris and Craig-y-Benglog. The Study of the Distribution of Floristically Rich Localities in Relation to Bed-rock. (With Plate 2 and two Maps in the Text) 167

Ian Hepburn. The Vegetation of the Sand Dunes of the Camel Estuary, North Cornwall. (With Plate 3 and one Figure in the Text) 180

R. Laird. The Influence of Soil Reaction on Rotation Grass in South-west Scotland 193

C. P. Petch. Vegetation of Roydon Common 143

C. B. Williams. Some Applications of the Logarithmic Series and the Index of Diversity to Ecological Problems. (With twenty-five Figures in the Text) . 1

M. Zohary. Outline of the Vegetation in Wadi Araba. (With one Figure in the Text) 204

NATURE CONSERVATION AND NATURE RESERVES 45

BRITISH ECOLOGICAL SOCIETY. Ecological Principles involved in the Practice of Forestry 83

REFERENCES IN THE BIOLOGICAL FLORA 116

REVIEWS

Journal of Animal Ecology (Vol. 12, No. 2) 130

An Introduction to Pollen Analysis 214

BIOLOGICAL FLORA OF THE BRITISH ISLES

Accounts Published or in Preparation 118, 253

Tamus L. by I. H. Burkill 121

Acer L. by E. W. Jones 215

Acer pseudo-platanus L. by E. W. Jones. (With Plate 4 and three Figures in the Text) 220

Acer platanoides L. by E. W. Jones 238

Acer campestre L. by E. W. Jones. (With three Figures in the Text) . . . 239

BRITISH ECOLOGICAL SOCIETY

Annual Meeting in the University Department of Botany, Oxford 131

List of Members 135

Accounts 257

VOLUME 32, NO. 1 MAY 1944

SOME APPLICATIONS OF THE LOGARITHMIC SERIES AND THE INDEX OF DIVERSITY TO ECOLOGICAL PROBLEMS

BY C. B. WILLIAMS, *Chief Entomologist, Rothamsted Experimental Station, Harpenden*

(*With twenty-five Figures in the Text*)

CONTENTS

PAGE
1. INTRODUCTION 1
2. PROBLEMS OF SPECIES, AREA AND NUMBERS OF INDIVIDUALS 3

Botanical:

Number of species of plants on a grassland area in Britain 3
Number of species of plants on areas of different sizes in an aspen association in North Michigan 5
Ground vegetation in *Tectonia* forest in Java 9

Zoological:

Distribution of head lice on a number of hosts 11
British nesting birds 13
Mosquitoes caught in a light trap in ten cities in Iowa, U.S.A. 14
Butterflies captured in Malaya by Dr A. S. Corbet 15
PAGE
3. PROBLEMS CONNECTED WITH THE GROUPING OF SPECIES INTO GENERA 17

Zoological:

Orthoptera of the world 17
Coccidae of the world 18
British insects 20
British birds 22

Botanical:

Flowering plants of the world . . 23
Grouping of genera into families . . 25
4. INDEX OF DIVERSITY IN DIFFERENT FAMILIES 26
Frequency of occurrence of different values of α 32
Classification of families of dicotyledons on index of diversity 33
5. GENERAL DISCUSSION 36
6. INDEX OF DIVERSITY USED AS A COMPARISON OF DIFFERENT POPULATIONS 42
7. SUMMARY 43
REFERENCES 44

1. INTRODUCTION

In a recent paper in the *Journal of Animal Ecology* (Fisher, Corbet & Williams, 1943) R. A. Fisher has discussed from the mathematical point of view the problem of the frequency of occurrence of species with different numbers of individuals in a random sample from a mixed population containing a large number of species; and in the same paper Corbet and myself have shown that Fisher's theories apply very well to observed random catches of large numbers of insects.

It had been previously noted on more than one occasion that if a sample of a number of individuals is taken from a mixed population, the number of species represented by only one individual will be comparatively high, the number of species represented by two individuals will be about half the number represented by one; the number represented by three individuals will be about one-third the number represented by one; and so on. This same distribution had also been stressed by Willis (1922) and Chamberlin (1924) in the frequency of the number of genera of plants and animals with one, two, three or more species.

Linlithgow Library

It had, however, been generally assumed that the 'hollow curve' thus formed could be best represented by the harmonic series of the form

$$n_1, \frac{n_1}{2}, \frac{n_1}{3}, \frac{n_1}{4}, \ldots, \text{etc.},$$

where n_1 is the number of groups with 1 unit.

Fisher *et al.* (1943), however, show that there is reason to believe that the facts are best represented by a logarithmic series

$$n_1, \frac{n_1}{2}x, \frac{n_1}{3}x^2, \frac{n_1}{4}x^3, \ldots, \text{etc.},$$

where x is a constant less than unity.

Several important biological and mathematical points follow from this. In the first place the new series, unlike the hyperbola, is convergent; and both the total number of groups (species) and the total number of units (individuals) are finite even for an infinite number of terms of the series. The total number of groups $= \frac{-n_1}{x} \log(1-x)$, and the total number of individuals $= \frac{n_1}{1-x}$. As there are two equations and only two 'unknowns' if we know for any sample the total number of species and the total number of individuals, we can rapidly find both n_1 and x, and hence can calculate the whole distribution.

Fisher has also shown a further development of great ecological interest. If a number of samples of different sizes be taken from the *same population*, it is found (both mathematically and by practical observation) that the ratio n_1/x is constant in all of them, and this ratio has been designated 'α' by Fisher.

It follows that if a sample is taken from a population, and the number of species and the number of individuals is counted, then n_1 and x can be calculated and from these α can be obtained. Once knowing α we can calculate the number of species that should be represented in any other sample of any size from the same population.

If α is large it indicates that the individuals are largely divided up into groups—there are more species for the same number of individuals. If α is small the individuals are divided up into fewer groups and, for the same number of individuals, the groups will be larger.

Since α expresses numerically the extent to which subdivision (or grouping) has taken place we have called it the 'Index of Diversity' of the population.

It is the purpose of the following paper to discuss the application of Fisher's logarithmic series and the index of diversity to a number of ecological problems connected with both botany and zoology and to show the wide application of the series to such problems, some of which have in the past been incompletely or only empirically explained.

It might be as well to begin by noting a few further points about the index of diversity:

(1) If several samples are taken from the same population, not only will they have the same index of diversity, but when two or more of them are added together the combined sample will still have the same index.

(2) Different populations may have, by chance, the same index of diversity, and samples from them will, of course, have the same α value. When these samples are added together, however, the α of the combined sample will be larger than that of either of the two or more original samples.

(3) If two populations are entirely apart—for example, a population of Geometrid and one of Noctuid moths; a population of Primulaceae and one of Violaceae; or plants in two widely separated areas with no species in common—then the α value of one sample from each combined will be the sum of the two α values for each sample separately.

If there is some overlap between the populations, as for example the flora of Spain and of England, the combined two samples will have an α value larger than either sample but smaller than the combined total. Thus the index of diversity of two combined samples, when compared with the values for the two samples separately, becomes a measure of the resemblance of the two populations from which the samples were obtained.

(4) If two samples, not of very small size, are taken from the same population the larger sample being p times the smaller, then the number of species in the larger sample will be $\alpha \log_e p$ more than in the smaller. It follows that if one sample is double the size of the other it will contain $0{\cdot}69\alpha$ more species (as $\log_e 2 = 0{\cdot}69$); and that α is the number of species added to a sample by multiplying its size by $e = 2{\cdot}718$.

This gives a method of finding the index of diversity of a population from two samples when their relative size, but not their absolute size in numbers of individuals, is known; as, for example, in the case of numbers of species on quadrats of different sizes. If two quadrats were used, one 1 m. sq. and the other 165 cm. sq. $(=\sqrt{2{\cdot}718})$, the difference in the average number of species in each would give α direct.

(5) For samples of different sizes for the same population x becomes gradually closer to unity as the size of the sample increases. For example, in the discussion below on British birds (p. 22), where the size of the sample is forty million pairs, $x = 0{\cdot}9999997182$. But we have seen that $n_1 = x\alpha$; so that as the size of a sample increases the number of species with one individual (or groups with one unit) gradually approaches α, but can never exceed it. The index of diversity of any population is therefore theoretically the limiting value of n_1, or the maximum number of species with one individual that can be obtained from one sample however large.

2. PROBLEMS OF SPECIES, AREA AND NUMBERS OF INDIVIDUALS

Botanical

Number of species of plants on a grassland area in Britain

G. E. Blackman (1935) gives the number of plants found on quadrats of different sizes in a grassland formation at Jeallots Hill, Bracknell, Berkshire, England, in August 1932. The data are shown in Table 1. It will be seen that the increase in number of species found by each successive doubling of the area is varying round 2·05; the first three values are rather below this figure.

Table 1

Size of quadrat in sq. in.	No. of species of plants	Additional no. obtained by doubling the area
2	5·9	—
4	7·8	1·9
8	9·5	1·7
16	11·1	1·6
32	13·6	2·5
64	16·1	2·5
128	18·2	2·1
	Av. increase	2·05

I have already shown (Fisher *et al.* 1943, p. 51) that, if the logarithmic series applies to a sample of a population, then the number of additional species obtained by doubling the size of the sample from the same population is approximately constant—provided the sample is not too small—and approximates to $\alpha \log_e 2$, which equals $0{\cdot}6931\alpha$ or alternatively $\alpha = 1{\cdot}443n$. If the sample is small the increase is less than this, but the smaller the value of α the smaller can be the size of the sample without large alteration in the size of the increase.

The figures in Table 1 give a definite indication that such conditions prevail, so that we can suggest that they represent samples from a population with an index of diversity rather above $1{\cdot}443 \times 2{\cdot}05$, or approximately 3·0.

If there is an average number of p plants per square inch in the quadrat then the actual number of individuals in each quadrat is p times the number of square inches; or, if we use the log of the number of individuals in the quadrat, it must equal $\log p + \log$ number of square inches. Hence for samples from any one population the log number of individuals = the log of the area + a constant.

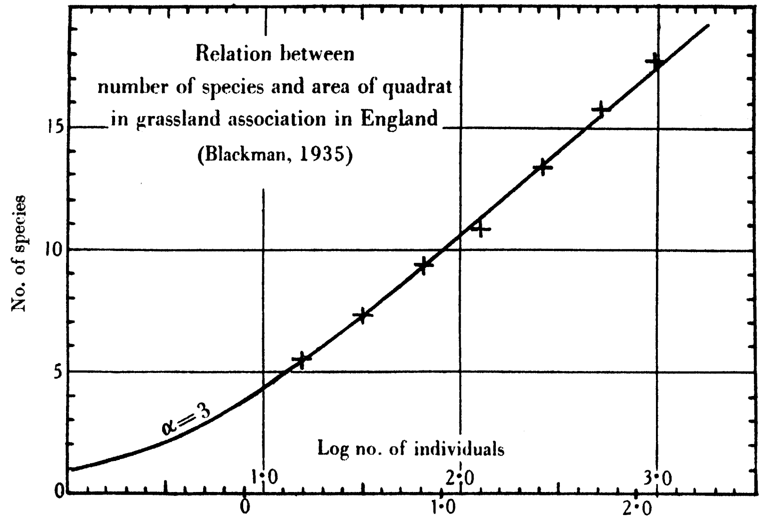


Fig. 1.

If we plot theoretically the log number of individuals against the number of species in various sized samples from a population with $\alpha = 3$ we get the line shown in Fig. 1.

If we take the log number of square inches in Blackman's quadrats and plot them against the number of species we get seven points almost in a straight line.

If to the log number of square inches in Blackman's quadrats we add 0·9 (= log of 8), these seven points fall almost exactly on the line for $\alpha = 3$ (Fig. 1).

Thus Blackman's results can be interpreted by the logarithmic series, and the index of diversity suggested by R. A. Fisher, on the assumption that we are dealing with a population with an index of diversity of 3 and with about 8 'individual plants' per square inch. This is about 288 per $6 \times 6n$ quadrat, 1152 per sq. ft. or 50 million per acre; or just over 1 plant per sq. cm.

It is not possible to say if these figures are anywhere near correct, as it is difficult in most plants to decide where an 'individual' begins or ends. It is interesting to note, however, that on p. 757 of Blackman's paper he indicates that the five dominant species on the area includes about 250 tillers per 6×6 quadrat. If we consider therefore a tiller as an individual, the suggestion that there should be 288 units of all plants on the quadrat is not inconsistent with reality.

Since we have already reached the portion of the curve where $\alpha = 3$ is practically a straight line, it is possible to make some interesting suggestions by extrapolation. Thus 1 acre = approximately $2^{22\cdot7}$ sq. in. The largest quadrat taken was 2^7 sq. in. and contained 18 species. By doubling this area 15·7 successive times we get 1 acre, and therefore if each doubling adds approximately 2·1 species, the acre should contain $18 + (2\cdot1 \times 15\cdot7)$ or approximately 52 species. Of these 3 should be represented by only one individual each (since α is the limiting value of n_1); about 10 species should be represented by 10 individuals or less, and about 15 species by 100 individuals or less.

Unfortunately, no record was taken at the time of the total number of species per acre, but Dr W. E. Brenchley informs me that it is not an unlikely number for an acre of fairly uniform natural grassland.

Number of species of plants on areas of different sizes in an aspen association in North Michigan

H. A. Gleason (1922) has discussed the number of species of plants which he found on 240 quadrats of 1 sq. m. each in an aspen association in North Michigan, U.S.A.

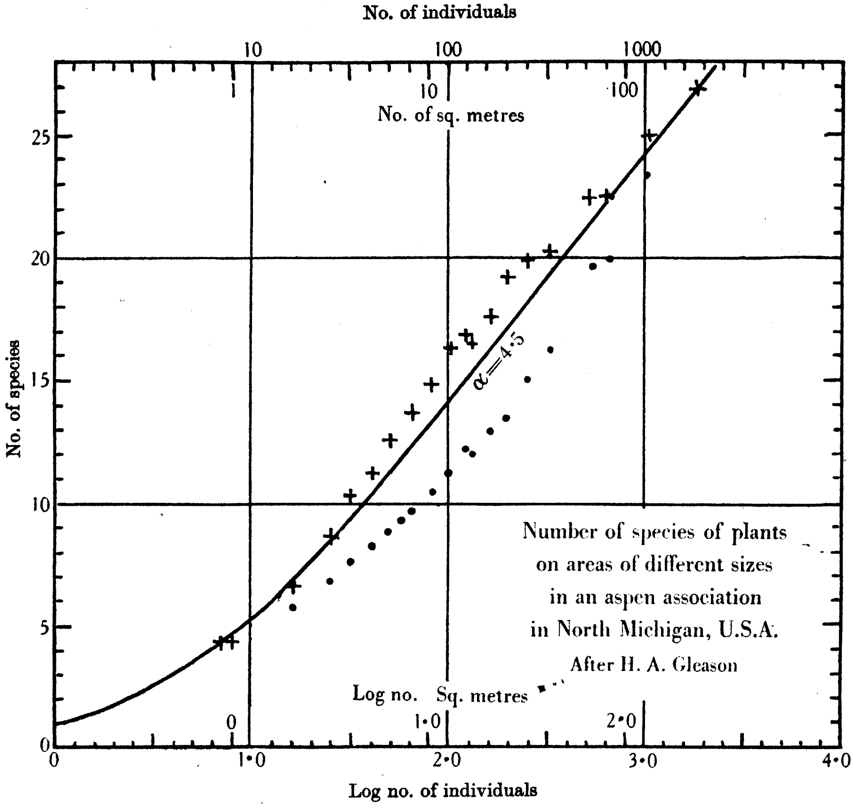
He first obtained the number of species on each of the 240 quadrats and then combined them in two different ways to get the number of species in larger areas. First, he found the average number of species in areas consisting of a number of contiguous quadrats; and secondly, he found the number of species in the same number of quadrats scattered as widely as possible over the whole area. His data is shown in Table 2. It will be seen that while the average number of species per quadrat (4·38) and the total number on the whole 240 quadrats (27·0) are the same for both series, the series showing contiguous areas rises more slowly at first than the scattered areas, but more rapidly later. This, according to Gleason, is due to the fact that the individuals of the different species are not truly randomized over the whole area, but numbers of one species tend to occur together. If the sample quadrats had been grouped by randomizing, the figures would be intermediate between the two results obtained.

Table 2. *Number of species of plants found on areas of different sizes in an aspen association in North Michigan. Data from H. A. Gleason*

	No. of species			No. of species	
Area in sq. m.	Contiguous quadrats	Scattered quadrats	Area in sq. m.	Contiguous quadrats	Scattered quadrats
1	4·38	4·38	16	12·00	16·67
2	5·82	6·67	20	12·92	17·67
3	6·90	8·75	24	13·50	19·40
4	7·60	10·37	30	15·13	20·00
5	8·21	11·29	40	16·17	20·33
6	8·95	12·65	60	19·75	22·75
8	9·67	13·80	80	20·00	22·67
10	10·33	14·88	120	23·5	25·00
12	11·25	16·25	240	27·0	27·00
15	12·25	16·94			

It should be noted that while the number of species for 1 sq. m. is the average of 240 estimations, the number of species in the 240 sq. m. is obtained only from a single observation and so is subject to a greater error.

Gleason's data are shown graphically in Fig. 2, the contiguous series by dots and the scattered series by crosses. The number of species is plotted against the log of the number of square metres covered by the sample. Gleason himself has pointed out that there is an approximately straight line relationship and he has extrapolated his results to suggest that there should be 56 species on the 25 sq. km. over which the formation extended.



Number of species of plants
on areas of different sizes
in an aspen association
in North Michigan, U.S.A.
After H. A. Gleason

Fig. 2.

He writes: 'Since the counted quadrats were located only in the treeless portions of the association, and since several additional species are confined to the aspen thickets, this theoretical result corresponds closely to the known total of approximately 80 species.'

It is interesting to note that if the relationship were a true straight line it could be extended in the opposite direction, with the curious result that in an area of about 0·4 m. there would be no species! This alone would make one suspect the validity of the straight-line association at very small values.

We notice from the table that an increase in the log number of square metres from 0 to 2·38 (an increase of 2·38) has been associated with an increase in the number of species from 4·38 to 27 (an increase of 23·63). If the linear relation holds an increase in the number of species corresponding to a log size of plot increase of 0·4342 ($=\log_{10} e$) would be 4·31. If the logarithmic series can apply to this data, then this is the value of α, or the index of diversity of the population (see p. 2). Since, however, we are dealing with rather small samples at first, α is probably rather larger than this.

If the curve of relation between numbers of species and log number of individuals for $\alpha=4{\cdot}5$ is superimposed on the previous sets of points for species and log number of square metres in the plot; and if the ordinates are shifted so that log 1 sq. m. corresponds to log 8 individuals (i.e. $=0{\cdot}9$) we get the fit shown in Fig. 2. The 'scattered quadrats' lie to the left of and above the line of $\alpha=4{\cdot}5$; the contiguous quadrats lie to the right and below. There is little doubt that truly randomized quadrats would give very close fit.

In other words, the data fit reasonably well to the theory of the index of diversity and the logarithmic series on the assumption that $\alpha=$ approximately 4·5 and that there are about 8 individual plants per sq. m. No information is available on this latter point, but there must be a comparatively small number, as on an average only 4·38 species are found per sq. m. This problem is of course complicated by the association of plants of the same species and the difficulty of deciding where an 'individual' plant begins and ends.

Table 3

Area in sq. m.	No. of repetitions	No. of species		
		Tract 1	Tract 2	Tract 3
1	256	4·82	4·88	3·06
4	64	10·69	10·67	7·31
16	16	17·38	19·00	14·81
64	4	25·00	28·00	22·75
256	1 only	32·00	33·00	31·0
Index of diversity	...	5·3	5·9	6·1

Table 4

Tract no. ...	4	5	6	7	8	9*	10†
Av. no. of species per sq. m.	4·19	4·62	4·75	4·15	4·15	2·93	3·73
Total species per 100 sq. m.	44	34	44	39	41	19	30
Total area of tract in sq. m.	8492	4350	8895	6142	44,331	6400	2500
Observed total flora	84	59	77	70	91	32	46
Total flora calculated by Gleason	82·4	58·1	82·3	70·2	89·8	33·5	48·3
Index of diversity	8·8	6·4	—	7·5	8·0	3·4	5·6

* Tract 9; in beech, sugar-maple forest of about 40 acres near shore of Lake Michigan in Emmet County.

† Tract 10; part of hardwood forest in Antrim County. Forest originally extended over 100 sq. miles.

If we extrapolate on this basis we get the number of species of plants on 25 sq. km. as 79, which is much closer to the observed figure than the calculation of Gleason; perhaps it is too high. Of these 79 species about four or five should be represented by only a single individual.

In a later paper Gleason (1925) gives further information about the aspen association in North Michigan, and other areas, to which the logarithmic series can be applied. His data is shown in a condensed form in Tables 3 and 4.

The data for the three aspen association tracts in Table 3 is shown diagrammatically in Fig. 3, fitted to curves for $\alpha=5$, 5·3 and 6. It will be seen that there is a very good fit for tract 1 to 5·3 and that tracts 2 and 3 are both close to $\alpha=6$.

In both 1 and 2 the number of species on 1 sq. m. corresponds to 0·9 on the log number of individuals, indicating a population density of about 8 individual plants per sq. m.

Tract 3, however, with an average of only just over 3 species per sq. m., fits best at a point indicating only about 4 plants per sq. m. Without fuller information about the plots it is difficult to say if this has any special meaning or any confirmation in the tract conditions.

Tracts 4–10, dealt with in Table 4, are shown diagrammatically in Fig. 4. In this case the horizontal ordinate is the log number of square metres in the sample. It will be seen that, as Gleason pointed out, an almost straight-line relationship exists between the different-sized plots on the same tract.

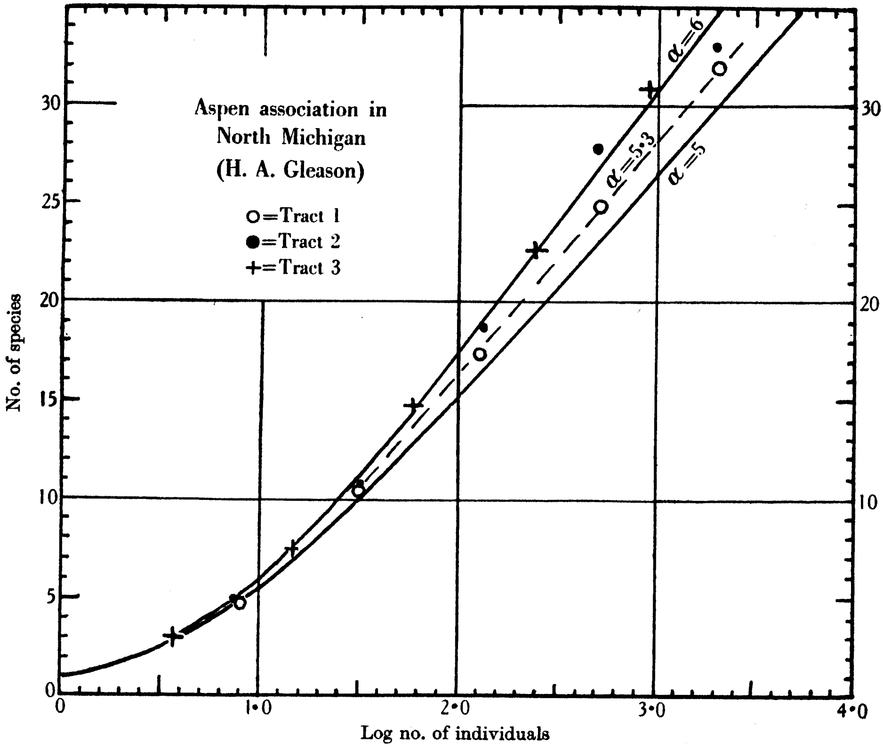


Fig. 3.

On the diagrams are marked by one or two short vertical lines the position on each line corresponding to the theoretical positions of 1000 and 10,000 individuals for the corresponding α values. It will be seen that in all cases except tract 4, the 1000 individuals line corresponds very closely to log 1·9 or 1·95, indicating that 1000 individuals is equivalent to between 80 and 90 sq. m., or 11–12 individuals per sq. m. Plot 4 indicates only about 8–9 plants per sq. m.

Plot 6 does not give a good straight line and has not been calculated.

Tracts 9 and 10, which give the two lowest figures for the index of diversity are, as seen from the notes to Table 4, from different plant associations from the remainder of the data.

Thus Gleason's additional data is consistent with the logarithmic series, with index of diversity ranging from about 3 to about 9, and an average density of population of about 10 plants to the square metre.

Ground vegetation in Tectonia *forest in Java*

O. Arrhenius (1923) gives details of the number of species of ground plants on areas of different sizes in different portions of a *Tectonia* forest in Java. His data is summarized in Table 5.

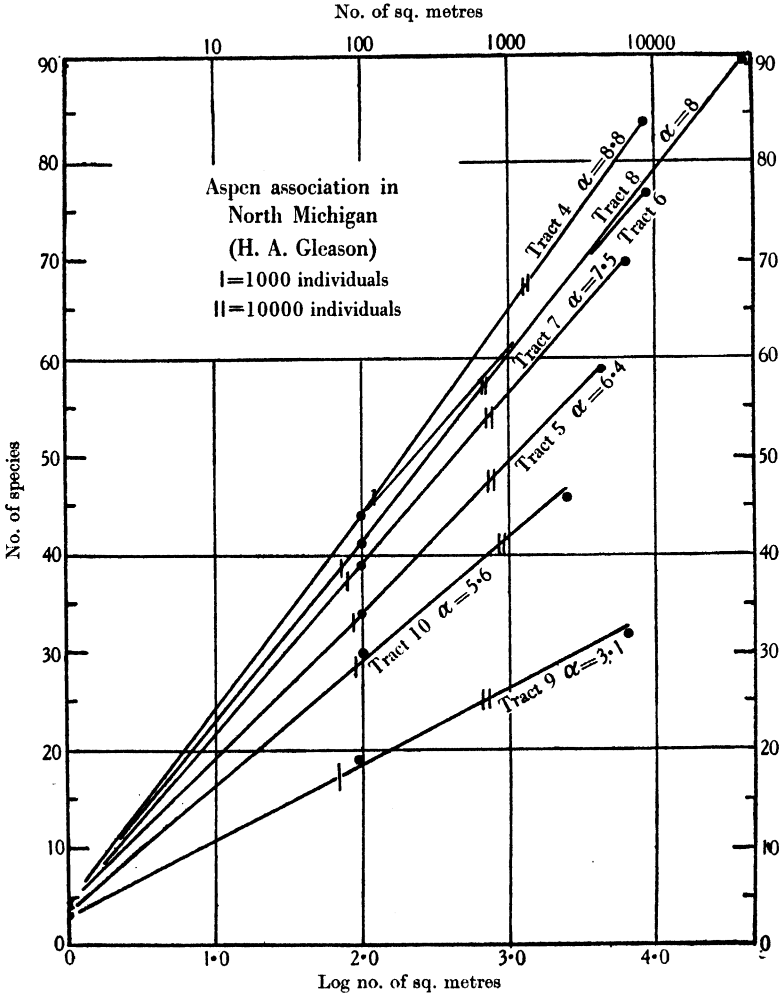


Fig. 4.

When the data of each survey number is plotted graphically the number of species against the log number of square inches in the area, it will be seen from Fig. 5 that each survey number gives an approximately straight line relationship. From this it is possible to estimate closely the index of diversity (α) (Table 5) and to draw the curves for these values on a number of species/log number of individuals basis.

The curves for the relation between number of individuals in the sample and number of species for the corresponding values of α are shown in Fig. 5, and the data for the plants are superimposed on these in the position of best fit.

Table 5. *Ground vegetation in* Tectonia *forest in Java* (after Arrhenius, 1923)

	No. of species observed						
Survey no. ...	18	26	33	21*a*	16*a*	23*a*	23*b*
Area in sq. m.							
100	40	23	18·6	15	15	5·7	4·5
200	56	33	26·4	21	22	8·6	6·7
300	66·8	39	—	—	27	—	—
400	75·0	44	36·9	29	30	12·1	10·0
500	—	—	—	—	—	13·5	11·5
600	86·3	51	—	—	36	—	—
700	—	—	—	37	—	—	—
800	—	—	47·0	—	41·5	16·2	14·6
900	97·0	58	—	—	—	—	—
1000	—	—	—	—	—	18·2	16·7
1200	103·7	64	—	—	49·5	—	—
1400	—	—	—	—	—	—	—
Index of diversity	29	18	15	12	—	7	8

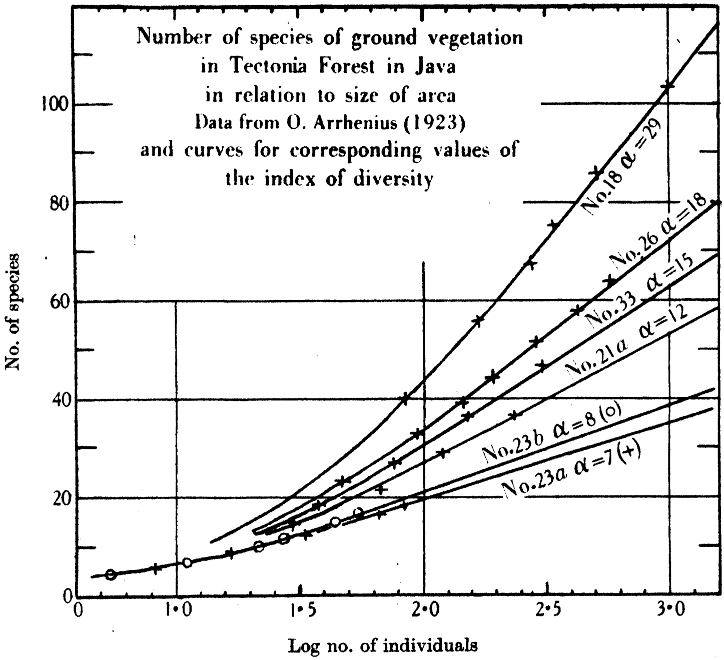


Fig. 5.

It will be seen first of all that the fit is exceptionally close, and secondly, that the position of the first observation in each survey plot, i.e. the number of species on 100 sq. m., to the number of individuals in the corresponding position on the α curve, differs in each plot.

Thus survey number 18 gives 40 species on 100 sq. m., and this on the α curve of 29 corresponds to about 95 individuals. That is to say that theoretically a population with an index of diversity of 29 would give 40 species if a sample of 95 individuals was taken.

The corresponding values for all the areas are as follows:

Survey nos.	No. of individuals corresponding to species on 100 sq. m.
18	95
26	47
33	37
21*a*	30
23*a*	5·5
23*b*	8

Thus the theoretical treatment suggests that there were many more individual plants per square metre in plot 18 than in plot 23. It is curious to note that, in all cases except the two plots 23*a* and 23*b*, the higher value of α is associated with a larger number of individuals per square metre.

Zoological

Distribution of head lice on a number of hosts

Dr P. A. Buxton kindly gave to me for study his records of the number of lice found on the heads of prisoners in the jail at Cannamore, South India (see P. A. Buxton, 1940).

Table 6 shows an analysis of the total number of lice of all stages on the heads of Hindu male prisoners in 1937, 1938 and 1939. The first column is the number of lice per head, and the second the number of heads in which that number of lice occurred. The third column are subtotals of every five groups followed by the total number of lice in the subtotal in brackets. Thus it will be seen that there were 622 heads free from lice; 106 heads

Table 6

No. of lice per head	No. of heads				No. of lice per head	No. of heads				No. of lice per head	No. of heads observed	
	Observed		Calculated			Observed		Calculated				
0	622									51	1	
1	106		107·15		26	4		2·87		53	1	
2	50		52·81		27	6		2·72		54	1	
3	29		34·69		28	2		2·59		57	1	
4	33		25·64		29	4		2·46		58	1	
5	20	238 (525)	22·22	240·51	30	1	17 (468)	2·35	12·98	59	1	
6	14		16·61		31	.		2·24		60	1	7 (392)
7	12		14·03		32	1		2·14		64	1	
8	18		12·10		33	5		2·04		66	1	2 (130)
9	11		10·60		34	.		1·95		71	1	
10	11	66 (521)	9·40	62·74	35	2	8 (267)	1·87	10·24	74	1	
11	3		8·43		36	2		1·79		79	1	
12	10		7·61		37	4		1·72		80	1	4 (304)
13	8		6·93		38	3		1·65		83	1	
14	6		6·34		39	.		1·58		88	1	2 (171)
15	3	30 (386)	5·83	35·13	40	4	13 (494)	1·52	8·26	110	1	
16	6		5·39		41	1		1·46		121	1	
17	7		5·00		42	.		1·41		128	1	
18	4		4·65		43	.		1·36		129	1	
19	7		4·34		44	2		1·31		145	1	
20	7	31 (560)	4·07	23·45	45	3	6 (264)	1·26	6·79	149	1	6 (782)
21	3		3·82		46	1		1·21		188	1	1 (188)
22	4		3·59		47	5		1·17		239	1	
23	4		3·39		48	1		1·13		270	1	2 (509)
24	4		3·20		49	.		1·09		303	1	
25	3	18 (414)	3·03	17·02	50	1	8 (379)	1·05	5·66	385	1	2 (688)

Total number of heads with lice, 461; total no. of lice, 7442.

with one louse each; and 525 lice distributed on the 238 heads which harboured from one to four lice inclusive.

Buxton had already (1938) shown that at various localities, individuals with fewer lice (1–10) were more frequent than those with more lice (10–100 or over 100), but no detailed study of the distribution had been made.

The data for Cannamore, exclusive of the number without lice, is shown graphically by the histogram in Fig. 6, and it will be seen immediately that it gives a curve of the 'hollow' type closely resembling a hyperbola. The same figure shows (as crosses) the data transformed to logarithmic co-ordinates, and it is then seen that the points do not fall on the straight line required by a hyperbola but agree well with the logarithmic series.

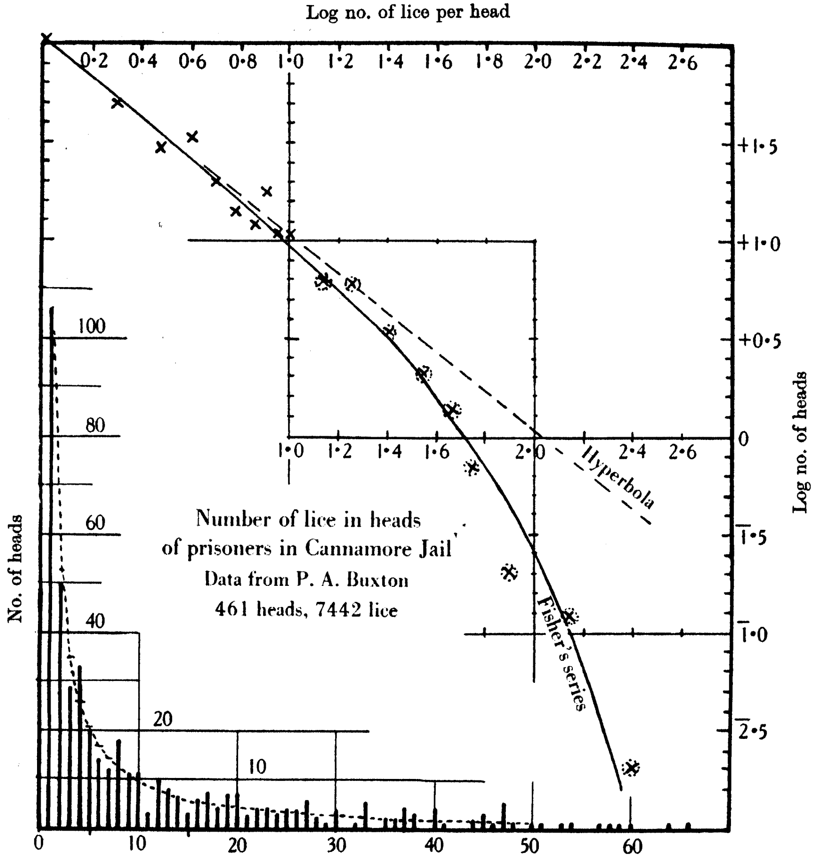


Fig. 6.

There were altogether 461 infested heads and on these were 7442 lice. From these two figures the corresponding logarithmic series can be calculated. It is found that $x = 0{\cdot}9856$ and $n_1 = 107{\cdot}15$. The very close resemblance of the calculated n_1 to the observed number, 106, is immediately noticed.

The calculated values for the series up to 50 lice per head, together with various subtotals, is shown in Table 6 and graphically on number and logarithmic basis superimposed on the figures in Fig. 6.

The remarkably close fit cannot be missed, particularly in the log transformation which is particularly accurate for small numbers. Thus, in addition to remarkably close resemblance in the number of heads with one louse already pointed out, the calculated number with 1–5 lice is 240·5 and the observed 238; the calculated number with 1–25 lice is 378·9 and the observed 383. Between 25 and 50 lice per head the fit is not so good, the observed figures being rather larger than the calculated.

There is no doubt that the two series are very close indeed, and it is difficult to believe that this resemblance is entirely accidental.

It may be mentioned that tests were made on the same data with other series. First the negative binomial was tested. This takes into account the number of heads (622) without lice, and with this series the number of heads with one louse was calculated to be 68·4, which is widely different from the observed number.

Secondly, a hyperbolic series was calculated to fit all the values (excluding free heads) up to 100 lice per head. This gave the number of heads with one louse as 86·8, again far from the observed value.

Thus the logarithmic series was closer to the observed than any other yet tested.

British nesting birds

Mr James Fisher has informed me that the most recent estimates of bird populations suggest that in May of any one year there are about 40 million pairs of nesting birds in England and Wales, and that these belong to about 170 species.

If the logarithmic series is applied to these figures we find that $x = 0{\cdot}9999997182$, that $n_1 = 11{\cdot}772$, and that α is the same as n_1 to about the 4th decimal place. From these data the figures in Table 7 have been calculated.

Table 7

Pairs per species	No. of species: At	No. of species: Up to	Individual % of total population: Up to
1	11·3	—	—
2	5·7	—	—
3	3·8	—	—
4	2·8	—	—
5	2·3	25·8	—
10	—	33·0	—
100	—	58·5	—
1000	—	84·2	—
10,000	—	136·3	3·28
1 million	—	159·8	24·6
2 million	—	164·9	43·1

It will be seen that there should be, according to the theory, about 11 species represented by only a single pair, about 26 species represented by less than 5 pairs, and about 58 species represented by less than 100 pairs.

At the other end there should be about 160 species represented by one million pairs or less, which leaves 10 species out of the original 170 which must be represented by more than one million pairs.

Unfortunately, the calculations for the rarer birds are difficult to check against observed figures, but Mr Fisher informs me that they are not unlikely results.

In the case of the common birds Fisher (1940, p. 102) has given a list of the estimated numbers of the common birds of England and Wales as shown in Table 8. It will be seen that he mentions 9 species of birds with about a million or more pairs as compared with a calculated figure of 10.

Table 8

	Nos. in millions	
	Nos.	Pairs
(1) Chaffinch	10	5
(2) Blackbird	10	5
(3) Starling	7	3·5
(4) Robin	7	3·5
(5) House sparrow	3	1·5
(6) Hedge sparrow	3	1·5
(7) Thrush	3	1·5
(8) Meadow pipit	3	1·5
(9) Rook	1·75	0·9

It is interesting to note, from the third column of Table 7, that, according to the calculations, all the individuals of species up to 100,000 pairs per species only constitute 3·28% of the total bird population; and that three-quarters of the total bird population is made up of the 10 species with more than a million pairs each. J. Fisher's figures in Table 8 suggest that the 9 commonest species comprise about 24 million pairs out of a total of 40 million or 60% of the population.

Mosquitoes caught in a light trap in ten cities in Iowa, U.S.A.

J. A. Rowe (1942) gives the number of mosquitoes caught by light traps in ten cities in the State of Iowa. The data is summarized in the first two columns of Table 9, and graphically in Fig. 7, where the log of the number of individuals in the sample is plotted against the actual number of species.

Table 9

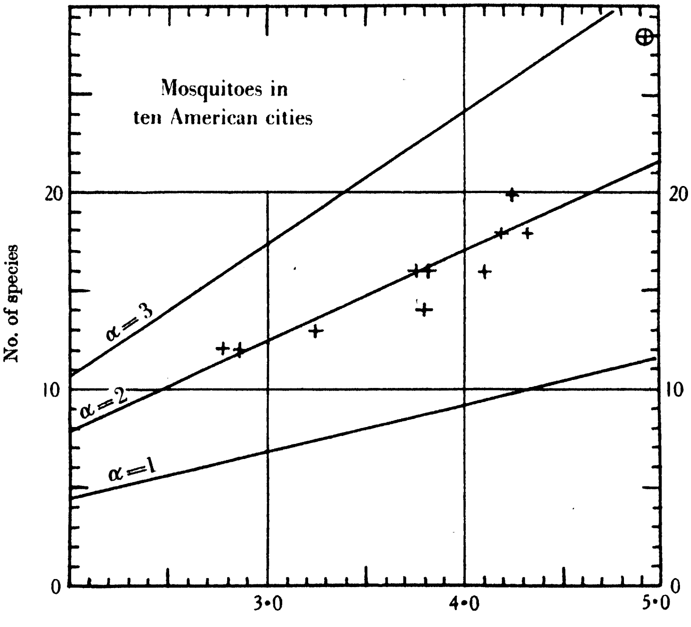
	No. of individuals	No. of species	Index of diversity
Ruthven	20,239	18	1·95
Des Moines	17,077	20	2·24
Davenport	15,280	18	2·02
Ames	12,504	16	1·81
Muscatine	6,426	16	1·98
Dubuque	6,128	14	1·71
Lansing	5,564	16	2·03
Bluffs	1,756	13	1·90
Sioux City	661	12	2·08
Burlington	595	12	2·13
Total	86,230	28	2·70

In the third column of Table 9 is shown the index of diversity (α) of each sample calculated from the logarithmic series. These are subject to a standard error of from 7·5 to 15% (i.e. approximately 0·15 to 0·3). The smaller error being in the larger samples. It will be seen that they are grouped closely round an average value of 2·0 and none differ significantly from this value.

To Fig. 7 has been added the curve showing the theoretical relationship of species and individuals for $\alpha=1$, 2 and 3, and the closeness of the fit of the different samples for $\alpha=2$ is apparent.

From this we can infer that the extent to which the individuals are diversified into species is more or less the same in all the cities. The small number of species caught in some cities and the larger number caught in others is almost exactly accounted for by the varying number of individuals captured.

When, however, all the ten catches are added together we get 86,230 individuals of 28 species showing an $\alpha = 2{\cdot}7$ which is significantly different from the average of 2·0 for the separate cities. From this we can infer that although the single cities are similar in their diversification, they have not identical populations. The area considered as a whole has a greater variety of species (and hence probably of environment) than any one of its parts.



Log no. of individuals
Fig. 7.

Butterflies captured in Malaya by Dr A. S. Corbet

The data obtained by Dr Corbet from a large collection of butterflies made in Malaya and already briefly discussed by him (Fisher *et al.* 1943, p. 42) provides an interesting problem in fitting incomplete data to the logarithmic series.

The collection was made by hand over a period of several years, and the important modification was that after Dr Corbet had caught about 25 specimens of a species he did not make regular attempts to get more. Thus up to about 25 specimens the data are a more or less random sample, but above this figure the number of individuals per species is consistently too low.

The data consisted therefore of three sets of information:

(1) The total number of species with less than 25 individuals per species was 501.

(2) The total number of species at all levels was 620.

(3) The total number of individuals at frequencies below 25 individuals per species was 3306.

The problem is to see if it is possible to obtain from this any values of x and n_1, that will give us the whole series.

From (1) we have $$n_1\left(1+\frac{x}{2}+\frac{x^2}{3}+\frac{x^3}{4}+\dots+\frac{x^{23}}{24}\right)=501.$$

From (2) we have $$n_1\frac{-\log\overline{1-x}}{x}=620.$$

From (3) we have $$n\,(1+x+x^2+x^3+\dots+x^{23})=3306.$$

From each of these equations it is possible to get a relation between n_1 and x. A number of these were calculated and lines through them are shown diagrammatically in Fig. 8.

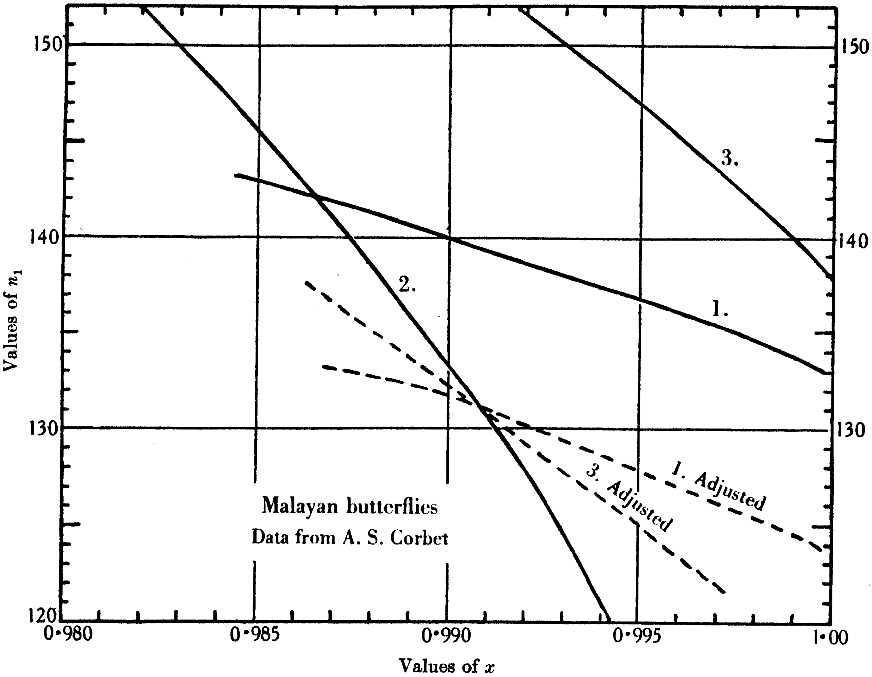


Fig. 8.

It will be seen that it is possible to find values for x and n_1, that will fit any two of the equations, but the three line relationships do not meet at a point and hence there is no values of x and n_1 that will fit simultaneously all three. Either the logarithmic series does not fit or there is some error in the data.

In view of the care taken in the identification the total number of species in the collection, 620, is probably very accurately determined. This means that the line of equation (2) is probably correct.

If the assiduity with which individuals were collected gradually fell off below the 24 individuals per species, instead of at or above this level, it would result in too many species (and hence too many individuals) being included in the 'below 25' category. If we agree that this might have taken place we can make a small reduction in the observed figures in equations (1) and (3).

If we reduce the observed species 'below 25' in equation (1) by 29 (just over 5%), and the observed individuals in equation (3) by 565 (which is just over 1 individual per species) we find that the lines for equations (1) and (3) in Fig. 8 are shifted to new positions as shown by the dotted lines, and that now all three lines meet approximately at the point represented by $n_1 = 131$ and $x = 0{\cdot}991$.

Otherwise the data can be made to fit the theory if we assume that there was a slight overestimation of the number of species and of individuals in the group below 25 individuals per species. The number of species below 25 individuals per species should have been about 472 and the number of individuals about 2841.

This is of course not proof of the fit of the theory to the observed facts, but it is interesting that the difference between the theory and the observed facts is in the direction of, and can be explained by, errors which might easily have occurred, and indeed Dr Corbet tells me that the assumption that assiduity in collecting fell off gradually before the 25 mark was reached is extremely probable.

3. PROBLEMS CONNECTED WITH THE GROUPING OF SPECIES INTO GENERA

Up to the present we have discussed the logarithmic series in relation chiefly to individuals grouped into species.

It has long been known that in many groups of plants and animals, the frequency of genera, with different numbers of species forms a 'hollow' curve of the hyperbolic type. The matter has been particularly discussed by Willis in his *Age and Area* (1922) and by Chamberlin (1924). Both writers assumed that the correct solution of the frequency distribution was the hyperbolic series and used this as a basis on which to formulate theories of evolution. Chamberlin unfortunately used also an incorrect method for obtaining the hyperbola to fit his data.

I have examined a number of sets of data of the frequency of genera with different numbers of species, in both animals and plants, and these are discussed below in relation to the logarithmic series.

Zoological

Orthoptera of the world

W. F. Kirby (1904–10) published a catalogue of the Orthoptera of the world based largely on his own studies with the collections at the Natural History Museum in London. When the number of genera with different numbers of species are tabulated the results are as shown in Table 10.

In the Acridiidae (short-horned grasshoppers) he describes 4112 species in 826 genera. This gives, on the basis of the logarithmic series, a calculated n_1 of $289{\cdot}3$, whereas the observed number is 320, about 10% above the calculated. For all genera containing four species or less the calculated number is 613 and the observed 639, which is within 4% of the calculated. The very close fit of the observed and calculated at higher values is best seen from the log scale in Fig. 9. There is no doubt whatever that the fit of the observed point to the calculated curve is very remarkable, and there is no evidence of a good fit to the hyperbola which is shown, transformed to log co-ordinates, on the same diagram.

In the Mantidae (Table 10 and Fig. 10) there were 805 species in 209 genera. This gives the calculated number of genera with one species as 82·27, as compared with the observed figure of 82! The figures for genera with up to 5 species per genus are 167 calculated and 169 observed, and the remarkably close fit at higher values is shown in Fig. 10.

In the Blattidae (Table 10) with 1612 species in 197 genera there is again a very close agreement between 54 observed and 57 calculated for the number of genera with one species. The rest of the fit is almost equally accurate; 127 calculated to 127 observed genera with 1–5 species; 29 calculated to 28 observed with 6–10 species; 14 calculated to 13 observed with 10–15 species, and so on.

In the Forficulidae (Table 10 and Fig. 11) there are much smaller numbers, only 480 species in 52 genera, but again the fit of calculated and observed is close. For genera with one species the figures are calculated 14·3 and observed 12, while for genera with up to 5, the calculated is 31·42 and the observed 31! The rest of the results are shown diagrammatically in Fig. 11.

Table 10. *Genera and species of Orthoptera of world* (from Kirkby, 1904–10)

No. of species per genus	ACRIDIIDAE		MANTIDAE		BLATTIDAE		FORFICULIDAE	
	Observed	Calculated	Observed	Calculated	Observed	Calculated	Observed	Calculated
1	320	289·3	82	82·27	54	56·80	12	14·3
2	131	134·5	28	36·93	30	27·39	9	6·94
3	86	88·35	27	22·11	16	17·62	5	4·49
4	61	58·11	12	14·88	14	12·75	2	3·26
5	41 (639)	43·21 (613·47)	20 (169)	10·69 (166·88)	13 (127)	9·88 (124·44)	3 (31)	2·53 (31·52)
6	27	33·47	7	8·00	5	7·91	3	2·05
7	21	26·68	4	6·16	6	6·54	—	1·66
8	18	21·70	8	4·84	7	5·52	1	1·44
9	23	17·94	4	3·86	8	4·74	—	1·25
10	17 (106)	15·01 (114·80)	1 (24)	3·12 (25·98)	2 (28)	4·11 (28·82)	— (4)	1·09 (7·49)
11	12	12·68	4	2·55	3	3·61	3	0·96
12	8	10·80	—	2·09	—	3·19	2	0·85
13	9	9·27	2	1·74	4	2·84	1	0·76
14	3	8·00	—	1·45	6	2·54	—	0·69
15	5 (37)	6·94 (47·69)	2 (8)	1·21 (9·04)	— (13)	2·29 (14·47)	1 (7)	0·62 (3·88)
16	4	6·05	1	1·02	2	2·07	—	0·56
17	3	5·30	—	0·86	4	1·88	—	0·52
18	6	4·65	—	0·73	1	1·71	2	0·47
19	2	4·10	1	0·62	2	1·57	—	0·44
20	3 (18)	3·62 (23·72)	1 (3)	0·53 (3·76)	— (9)	1·44 (8·67)	— (2)	0·40 (2·39)
21	1	—	—	—	4	1·32	1	—
22	1	—	—	—	—	1·21	—	—
23	2	—	—	—	—	1·12	—	—
24	1	—	—	—	1	1·04	—	—
25	— (5)	—	—	0·25	1 (6)	0·96 (5·65)	— (1)	—
26	2	—	—	—	4	0·89	—	—
27	—	—	—	—	1	0·83	—	—
28	—	—	—	—	2	0·77	—	—
29	4	—	—	—	—	0·72	1	—
30	— (6)	—	— (0)	—	— (7)	0·67 (3·88)	1 (2)	—
	Also 2 at 31 and 34 and single genera at 35, 36, 38, 41, 43, 51, 54, 58, 72, 75, 103 and 202		Also 2 at 30		Also at 31, 40, 44, 48, 56, 85 and 160		Also at 32, 35 (2), 36 and 47	
	Total: 4112 species in 826 genera		Total: 805 species in 209 genera		Total: 1612 species in 197 genera		Total: 480 species in 52 genera	
	$\alpha = 311{\cdot}2$, $x = 0{\cdot}92964$		$\alpha = 91{\cdot}62$, $x = 0{\cdot}89781$		$\alpha = 58{\cdot}89$, $x = 0{\cdot}96476$		$\alpha = 14{\cdot}83$, $x = 0{\cdot}97003$	

Coccidae of the world

Two catalogues of the Coccidae of the world have been examined. Fernald (1903) recognized 1439 species in 166 genera. MacGillivray (1921) increased the number of known species to 1762, but more than doubled the genera to 352. The frequency of genera of different size according to each author is shown in Table 11, and diagrammatically on the log scale in Fig. 12.

It will be seen that in both cases the observed number of genera with one species is well above the calculated: in the case of MacGillivray's classification it is nearly 50% above. Genera with 2, 3, 4 and 5 species are, however, in MacGillivray's case all below

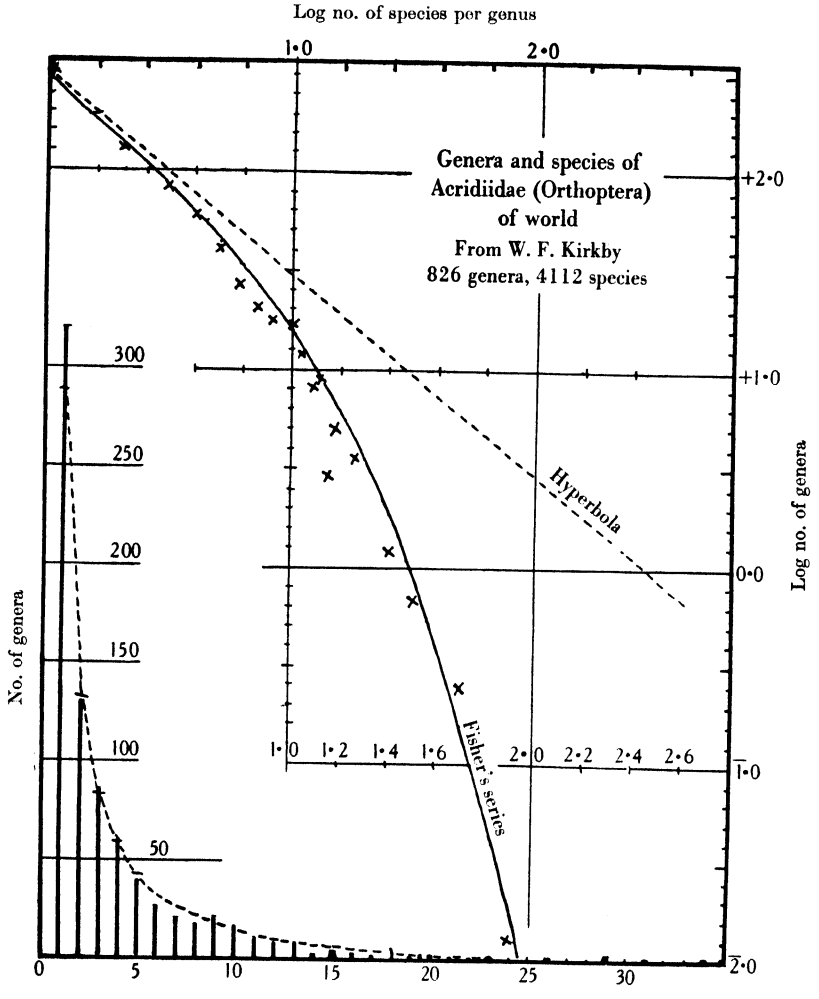


Fig. 9.

the calculated, so that the difference on all genera with up to 5 species is only 282 observed to 259 calculated, an excess of about 9%. It will be seen from Fig. 12 that although the points are variable and more off the theoretical curve than in the case of Orthoptera, yet the logarithmic series does generally represent the form of the curve, and is much closer to the truth than is the hyperbola.

British insects

In 1904 Beare and Donisthorpe published a catalogue of the British Coleoptera. They recognized 3268 species in 804 genera (Table 12, 1st column). Calculations from these two figures give the series shown in the same table and diagrammatically in Fig. 13. It will be seen that the observed number of genera with one species is about 20% above the calculated, but that all the other genera with from 2 to 10 species are below so that the calculated number of genera with up to 10 species, 733, is almost identical with the calculated 734·4. The general close resemblance of the observed and calculated figures is well shown on the logarithmic curve in Fig. 13.

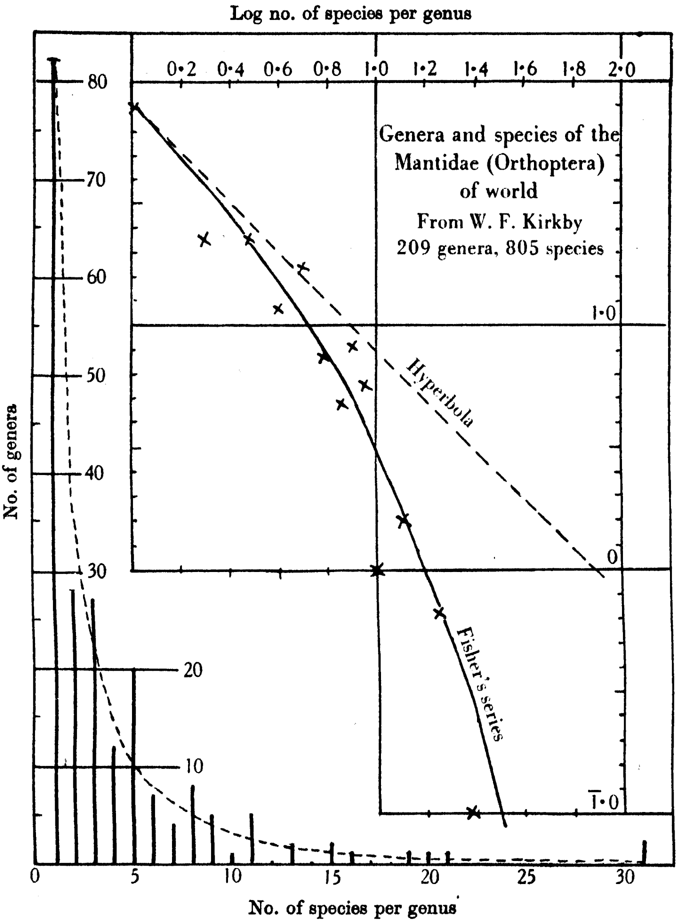


Fig. 10.

In 1857 Stainton published a list of the British Lepidoptera. He recognized 1902 species in 499 genera. This gives a calculated n_1 of 197·4 as against an observed 243 (Table 12, 2nd column); but again, as in the Coleoptera, every other value from 2 to 10 species per genus the observed is below the calculated, so that the total observed (468) and calculated (461) figures to 10 species per genus are very close indeed. The results are shown graphically in Fig. 14.

In the last two columns of Table 12 and in Fig. 15 is shown a comparison of the figures for Macrolepidoptera (excluding butterflies), according to Stainton's 1857 catalogue and the most recent classification by Edelsten in the 1939 edition of South's *Moths of the British Isles*. Stainton recognized 703 species in 249 genera; Edelsten has 713 species in 357 genera. It will be noted that an increase of only 10 species has been accompanied by an increase of over 100 genera. It will be seen that the calculated number of genera with one species is in both cases below the observed, but again the following genera in the series are rather below so that either up to 5 or up to 10 species per genus there is a very close agreement. The results are shown graphically, in a logarithmic scale only, in Fig. 15, when it will be seen that Stainton's classification is more regularly consistent with the calculated series than is the more recent classification of Edelsten. The possible meaning of this will be discussed later.

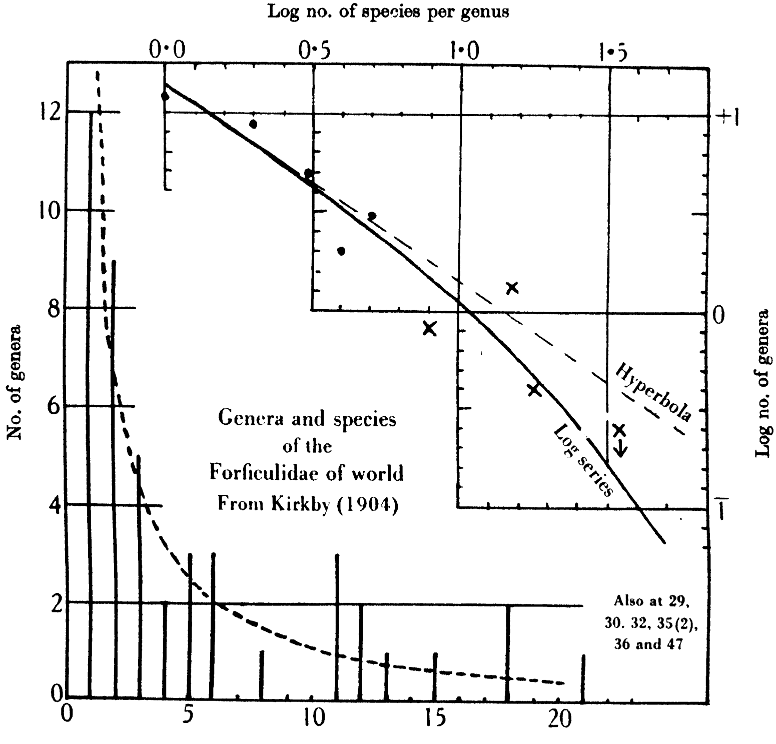


Fig. 11.

In 1896 Edwards published a monograph containing families of the British Homoptera in the Cicadina (excluding Psyllidae); he recognized 271 species in 48 genera. Quite recently Dr C. G. Butler has given me a MSS. list showing the most recent classification of the same group, based, I understand, on discussions between himself and Mr China.

The list includes 360 species in 73 genera (Table 13 and Fig. 16). Both series agree fairly well with the calculated, though in each case the observed n_1 is greater than the calculated; the difference, however, is smaller than in the previous groups. If all genera up to 5 species per genus are considered the agreement is very close; 34 calculated to 32 observed for Edwards, and 54 calculated to 53 observed for Butler and China. Again the logarithmic graphs in Fig. 16 show how much closer the observed results are to the logarithmic series than to the hyperbola.

Table 11. *Frequency of genera with different number of species in the scale insects (Coccidae) of the world*

No. of species per genus	MacGillivray		Fernald	
	Observed	Calculated	Observed	Calculated
1	181	122·98	65	46·90
2	42	57·20	18	22·69
3	22	35·47	16	14·63
4	21	24·73	8	10·61
5	16 (282)	18·41 (258·79)	5 (112)	8·22 (103·05)
6	6	14·28	5	6·62
7	5	11·39	7	5·49
8	7	9·27	3	4·65
9	5	7·66	3	4·00
10	4 (27)	6·42 (49·02)	2 (20)	3·48 (24·24)
11	6	5·43	1	3·06
12	5	4·63	5	2·71
13	4	3·97	—	2·42
14	2	3·43	1	2·18
15	6 (23)	2·98 (20·44)	2 (9)	1·97 (12·34)
16	—	2·60	1	1·78
17	1	2·28	2	1·62
18	1	2·00	2	1·48
19	—	1·76	1	1·36
20	2 (4)	1·56 (10·20)	1 (7)	1·25 (7·49)
21	1	1·38	—	1·15
22	—	1·23	1	1·06
23	—	1·09	—	0·98
24	2	0·97	—	0·91
25	1 (4)	0·87 (5·54)	1 (2)	0·85 (4·95)
26	—	—	—	—
27	2	—	1	—
28	2	—	2	—
29	—	—	1	—
30	4 (8)	—	1 (5)	—

Also at 31, 60, 70 and 200
Total: 1762 species in 352 genera
$\alpha = 132{\cdot}2$, $x = 0{\cdot}93024$

Also at 33, 34, 37, 57, 59, 62 (3), 70, 79 and 99
Total: 1439 species in 166 genera
$\alpha = 48{\cdot}47$, $x = 0{\cdot}96741$

British birds

In 1941 Witherby, Jourdain, Ticehurst and Tucker published, in the last volume of their handbook, a check list of the British Birds. They recognize 198 genera containing 424 species, or 420 species and subspecies. Table 14 and Fig. 17 shows the calculated and observed results for both these sets of figures. In each case there is no doubt as to the general close fit of the logarithmic series to the observed data, but again the observed n_1 is above the calculated. Again also if we take all genera up to 5 species per genus the fit is very close indeed; 192 observed to 186 calculated for species only, and 177 observed to 175 calculated if both species and subspecies are included.

Thus we can say that, in the Zoological Kingdom, the logarithmic series closely represents the frequency of genera with different numbers of species, except there is a tendency for the calculated number of genera with one species to be below the observed.

Botanical

Flowering plants of the world

J. C. Willis in his *Age and Area* (1922) has already drawn attention to the fact that the frequency of the number of genera of plants with different numbers of species forms a 'hollow curve'.

The first column of Table 15 and Fig. 18 show data obtained by taking the first one thousand genera of flowering plants and ferns from the same author's *Dictionary of Flowering Plants and Ferns* (1925 ed.). The number of species in each genus is given accurately when small, but the larger numbers are unfortunately only approximate, as will be seen from the fact that there are 54 genera mentioned with 10 species, but only 4 with 9, and 3 with 11; again at 20 species per genus there are 37 genera listed, but none at either 19 or 21. The figures will, however, probably serve their purpose, as the higher numbers can be averaged.

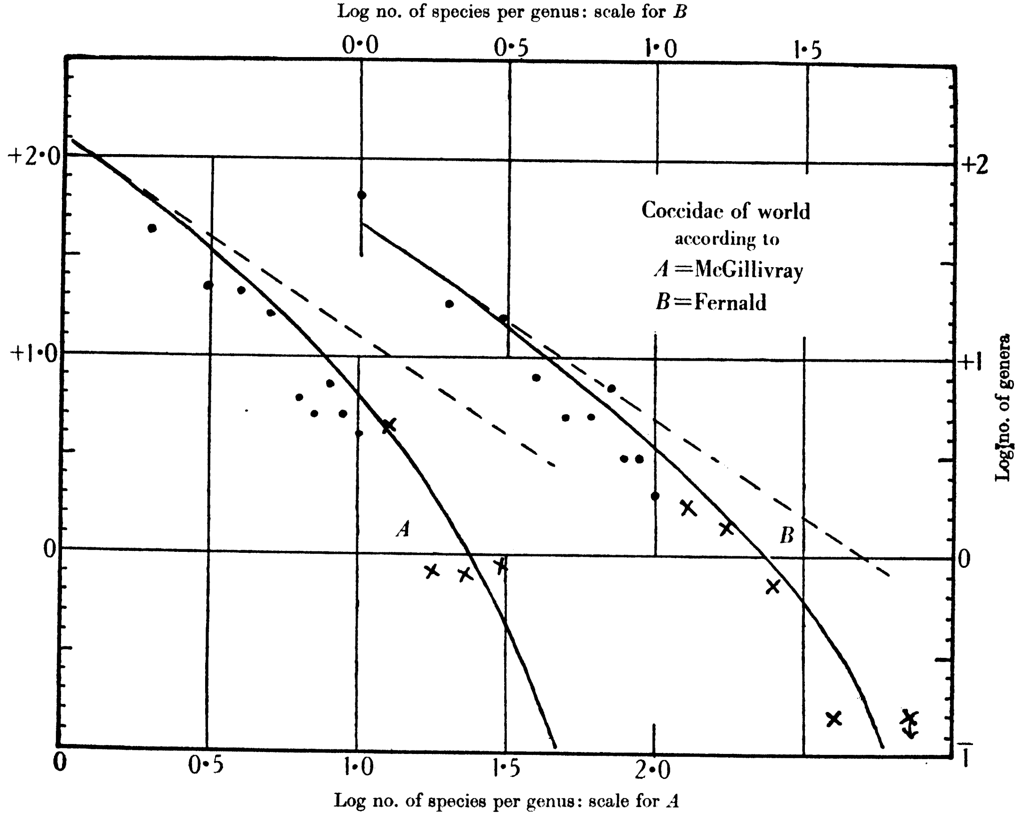


Fig. 12.

In all there were 15,473 species in the 1000 genera. This gives by calculation $\alpha = 238{\cdot}9$, $x = 0{\cdot}98475$ and n_1 (the number of genera with one species) as 235·34. The observed figure for the latter was 309, so that once again the observed n_1 is higher than the calculated.

The observed n_2 is also a little larger than the calculated, but after that the fit becomes good and the number of genera with 6–10 species is 136 observed and 137 calculated.

Fig. 18 shows that there are also rather too many genera with large numbers of species than the calculations predict. In fact, for the first time one might suggest that a straight line (shown dotted) might fit the observed results as well as the log series. The hyperbola is however definitely ruled out as in all other cases.

Table 12. *Frequency of genera with different number of species in British insects*

No. of species per genus	British Coleoptera (Beare & Donisthorpe, 1904)		British Lepidoptera (Stainton, 1857)		British Macrolepidoptera (excl. Butterflies)			
					From Stainton (1857)		From South & Edelsten (1939)	
	Observed	Calculated	Observed	Calculated	Observed	Calculated	Observed	Calculated
1	391	308·5	243	197·4	132	112·13	239	203·4
2	126	139·7	75	88·47	40	47·12	51	72·68
3	75	84·35	49	52·85	25	26·40	25	34·62
4	48	57·28	35	35·52	12	16·64	12	18·56
5	29 (669)	41·50 (631·33)	21 (423)	25·47 (399·71)	13 (222)	11·19 (213·48)	8 (335)	10·61 (339·87)
6	20	31·32	17	19·02	8	7·84	3	6·32
7	18	24·31	5	14·31	3	5·64	4	3·87
8	10	19·26	9	11·46	3	4·15	3	2·42
9	10	15·51	8	9·13	3	3·10	2	1·54
10	6 (64)	12·65 (103·06)	6 (45)	7·36 (61·28)	— (17)	2·35 (23·08)	3 (15)	0·99 (15·14)
11	14	10·40	4	6·00	3	1·79	1	0·64
12	7	8·63	4	4·93	—	1·38	—	0·42
13	6	7·22	2	4·08	1	1·07	1	0·28
14	4	6·07	1	3·39	—	0·84	—	0·18
15	4 (35)	5·13 (37·45)	4 (15)	2·84 (21·24)	2 (6)	0·66 (5·74)	1 (3)	0·12 (1·64)
16	5	4·36	—	2·38	—	0·52	—	0·08
17	4	3·71	1	2·01	—	0·41	2	0·06
18	—	3·18	1	1·70	1	0·32	1	0·04
19	4	2·73	1	1·45	—	0·26	—	0·03
20	— (13)	2·34 (16·32)	— (3)	1·23 (8·77)	— (1)	0·21 (1·72)	— (3)	0·02 (0·23)
21	3	—	—	—	—	—	—	—
22	1	—	1	—	—	—	—	—
23	—	—	1	—	1	—	—	—
24	2	—	—	—	—	—	—	—
25	1 (7)	1·14	— (2)	—	— (1)	—	— (0)	—
26	1	—	1	—	1	—	—	—
27	—	—	1	—	—	—	—	—
28	1	—	1	—	—	—	—	—
29	—	—	—	—	—	—	—	—
30	1 (3)	0·58	— (3)	—	— (1)	0·024	— (0)	—
	Also at 31, 33, 35, 37 (2), 39, 40, 47, 53, 64, 77 and 155		Also at 32, 39, 40, 41, 43, 45, 53 and 101		And one at 40		And one at 43	
	Total: 3268 species in 804 genera		Total: 1902 species in 499 genera		Total: 703 species in 249 genera		Total: 713 species in 357 genera	
	$\alpha = 340{\cdot}7$, $x = 0{\cdot}90559$		$\alpha = 220{\cdot}3$, $x = 0{\cdot}89620$		$\alpha = 133{\cdot}4$, $x = 0{\cdot}840506$		$\alpha = 284{\cdot}59$, $x = 0{\cdot}7147$	

Two examples of the relation of genera and species in the British flowering plants are shown in the last two columns of Table 15 and in Fig. 19. They are from the *Floras* of Bentham & Hooker (1906 ed.), who recognized 1251 species in 479 genera, and of Babington (1922 ed.), who recognized 1671 species in 511 genera.

It will be seen, particularly from the diagrams, that the fit to the logarithmic series is in general good, except that once more the observed numbers of genera with one species is higher than the calculated. The hyperbolic series is ruled out, and there is no suggestion that any other straight line would pass through the points on the logarithmic transformation.

Grouping of genera into families

If we consider the frequency of the different number of genera in higher groups such as families we once more get data which fit in closely with the logarithmic series.

Table 16 and Figs. 20 and 21 show series of the number of families with different number of genera in the flowering plants of the world, in the British flora and the flora of Colorado. The data for the plants of the world from Rendle (1925) is shown in the first column of Table 16 and in Fig. 20. It is of interest, as it is the first case we have dealt with here where the observed n_1 is distinctly below the calculated. In fact, all except one of the first five figures are below the calculated. To balance this there is, as will be best seen from the diagram, a slight excess of observed genera with 10–100 species. On the whole, however, the log series is not an unreasonable fit. The two sets of data for the British flora are shown in the second and third columns of Table 16 and in Fig. 21. In each case the fit is good in view of the irregularity of the points, and it is most certainly unlikely

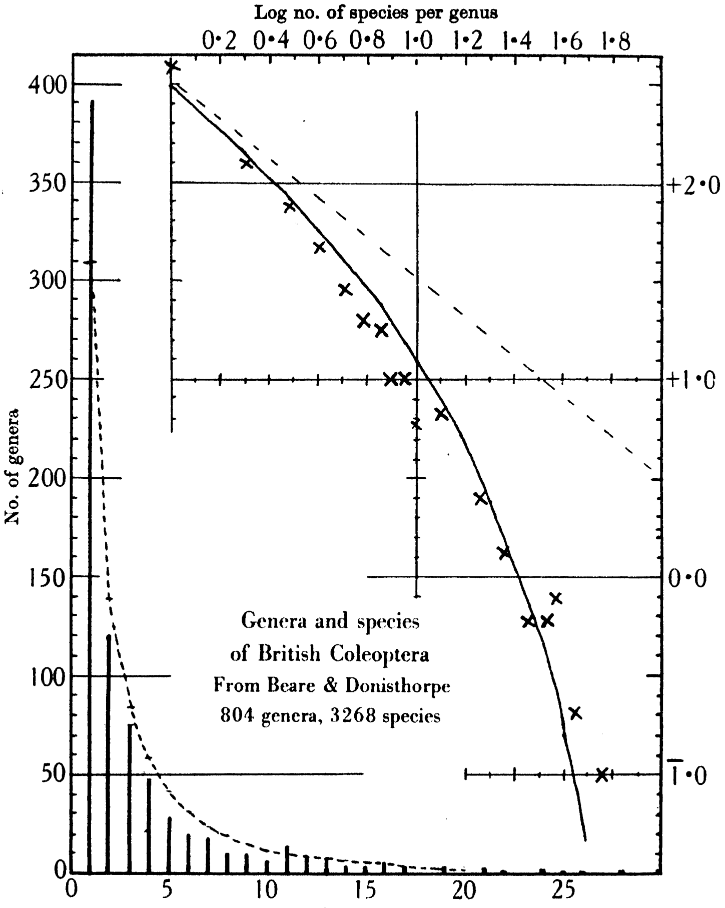


Fig. 13.

that any other simple curve would give a better fit. In each case, unlike Rendle's data for the world, there is a slight excess of observed families with a single genera over the calculated.

The data for Colorado (Fig. 20 and the last column in Table 16) are again a very close fit to the logarithmic series; n_1 is observed to be 46 and calculated 43; n_2 is rather above the calculated, but this is balanced by n_3, n_4 and n_5 all being below. The higher observed values, as will be best seen from the diagram, are a very close fit to calculated figures.

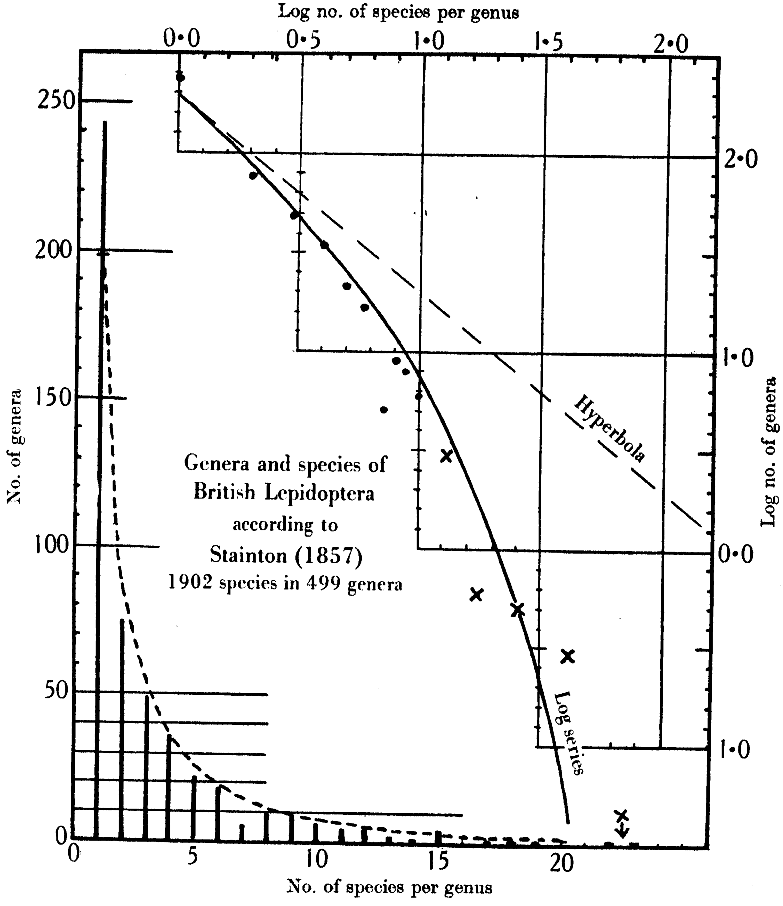


Fig. 14.

4. INDEX OF DIVERSITY IN DIFFERENT FAMILIES

Since the index of diversity, α, is a measure of the extent to which the units under discussion are collected into larger groups, it might be interesting to see to what extent the process of grouping species into genera, or splitting genera into species, has gone on in different families of plants and animals.

It must be recalled that a higher value of α means that the same number of units are divided into more groups, i.e. in the present case it means that the same number of species will be classified into more genera, with of course fewer species per genus, unless the 'sample' is larger. A low value of α means fewer genera with a higher average number of species per genus.

The same α value for species with different numbers of units means that the increase in the number of genera can be accounted for by the sampling processes involved in selecting a larger number of units. For the same index of diversity a large number of species will be divided into 'proportionally' fewer genera with more species in each, than will be the case with a small number of species.

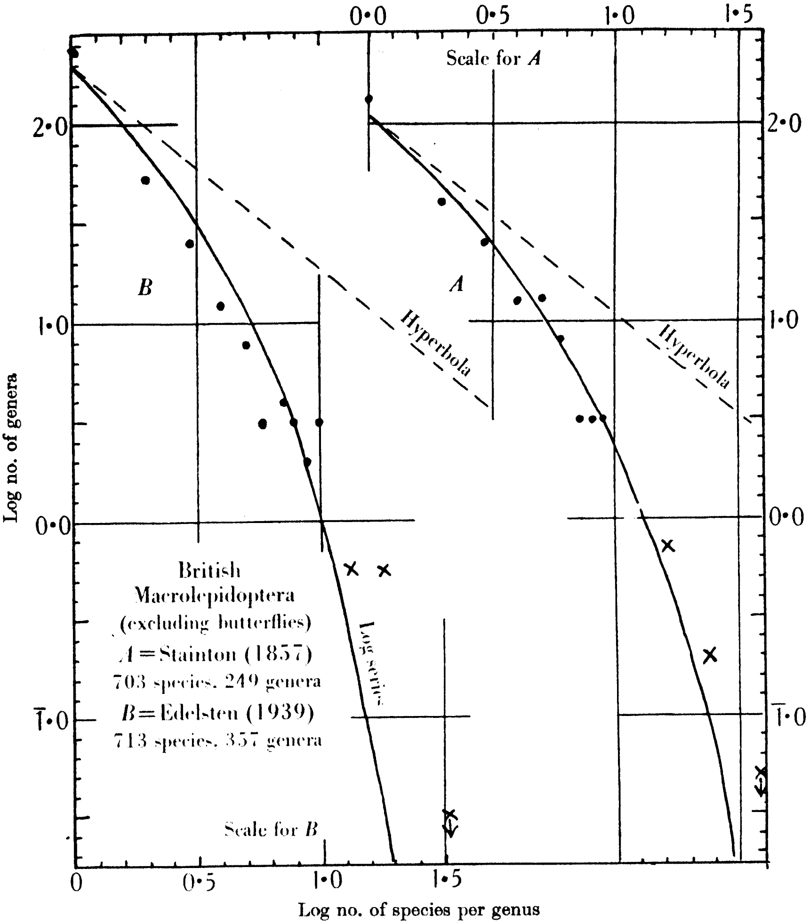


Fig. 15.

Fig. 22 shows the log number of species and the number of genera in 35 subfamilies of the Orthoptera of the world from Kirkby's catalogue. On the same diagram are lines showing the expected relationships for different values of α. It will be seen that index of diversity varies in the different subfamilies from below 1 to about 120; and that in general the families with more genera and species have the higher index. Subfamilies with under

Table 13. *Frequency of genera with different numbers of species of British Cicadina according to Edwards* (1894–6) *and Butler & China* (1942 *MSS.*)

No. of species per genus	Edwards (1896)		Butler & China (1942)	
	Observed	Calculated	Observed	Calculated
1	19	15·94	33	25·7
2	9	7·50	10	11·93
3	2	4·73	5	7·39
4	2	3·32	3	5·15
5	— (32)	2·50 (33·99)	2 (53)	3·82 (53·99)
6	2	1·96	4	2·96
7	2	1·58	3	2·36
8	2	1·30	2	1·91
9	2	1·09	2	1·58
10	— (8)	0·92 (6·85)	— (11)	1·32 (10·13)
11	1	0·79	—	1·12
12	2	0·68	1	0·95
13	—	0·59	1	0·81
14	—	0·52	—	0·70
15	1 (4)	0·45 (3·03)	2 (4)	0·61 (4·19)
16	—	0·40	—	0·53
17	—	0·36	—	0·46
18	1	0·32	—	0·41
19	—	0·28	—	0·36
20	— (1)	0·25 (1·61)	1 (1)	0·32 (2·08)
	Also at 26 and 56		Also at 21 (2), 33 and 41	
	Total: 271 species in 48 genera		Total 360 species in 73 genera	
	$\alpha = 16{\cdot}94$, $x = 0{\cdot}94117$		$\alpha = 27{\cdot}65$, $x = 0{\cdot}92867$	

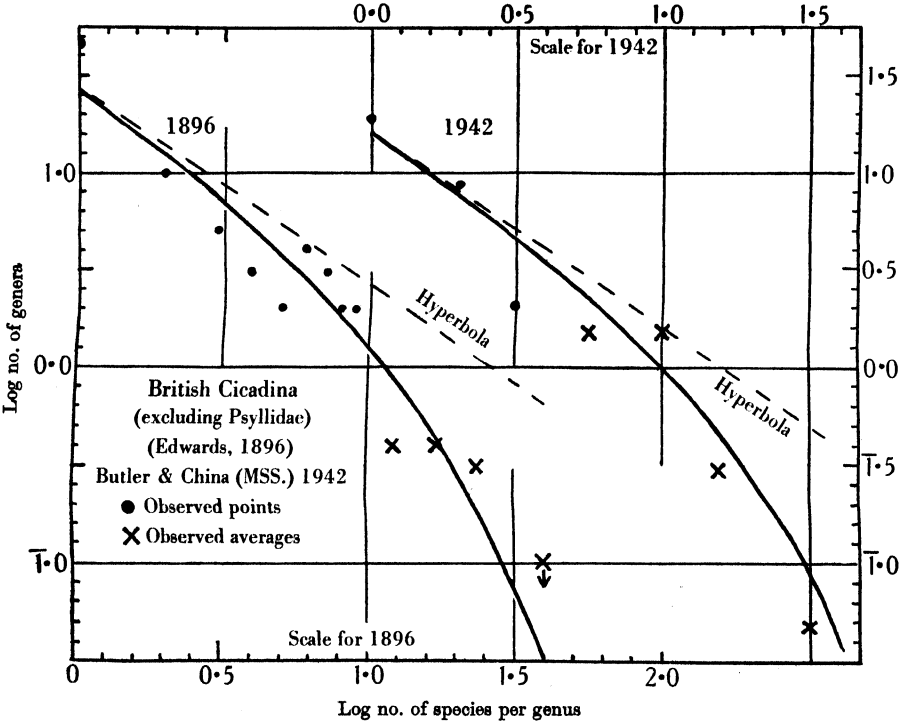


Fig. 16.

Table 14. *Frequency of genera with different numbers of species in British Birds according to Witherby, Jourdain, Ticehurst and Tucker (vol.* 5), 1941

No. of species in genus	Species only		Species and subspecies	
	Observed	Calculated	Observed	Calculated
1	121	107·8	107	93·08
2	34	40·21	32	38·68
3	12	19·99	17	21·43
4	10	11·18	19	13·36
5	15 (192)	6·67 (185·85)	2 (177)	8·88 (175·43)
6	3	4·15	2	6·15
7	5	2·65	3	4·38
8	1	2·17	2	3·18
9	3	1·15	3	2·35
10	1 (13)	0·77 (10·89)	1 (11)	1·76 (17·82)
11	1	0·45	5	1·33
12	1	0·35	1	1·01
13	1	0·26	4	0·78
14	—	0·17	—	0·60
15	— (3)	0·12 (1·35)	1 (11)	0·46 (4·18)
	Total: 424 species in 198 genera		Total: 520 species and subspecies in 198 genera	
	$\alpha = 144{\cdot}56$, $x = 0{\cdot}7457$		$\alpha = 112{\cdot}01$, $x = 0{\cdot}8310$	

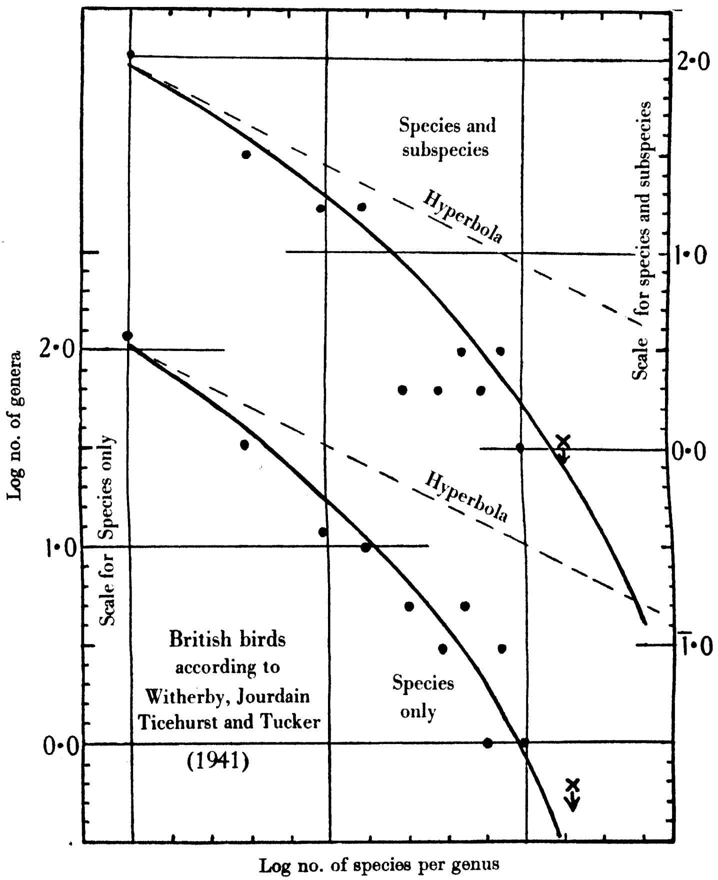


Fig. 17.

100 species nearly all have indices below 10; subfamilies with between 100 and 1000 species have indices from 5 to 50, and the only subfamily with over 1000 species has an index of about 120.

The general interpretation is that the larger subfamilies have more genera and fewer species per genus than would be expected if they were merely larger samples for a population of a similar make up to those from which the smaller families are drawn. On the other hand, some quite large families, e.g. the Phyllodrominae with 463 species and 26 genera, have a relatively low index, as compared with the Truxalinae with 641 species and 141 genera.

Table 15. *Frequency of genera and species of flowering plants*

No. of species per genus	Plants and ferns of world (Willis, 1000 genera)		British flowering plants Babington, 1922 ed.)		British flowering plants (Bentham & Hooker, 1906 ed.)	
	Observed	Calculated	Observed	Calculated	Observed	Calculated
1	309	235·34	255	217·75	256	231·3
2	126	115·9	93	94·69	84	94·3
3	77	76·08	45	54·89	51	51·3
4	37	56·18	37	35·96	22	31·3
5	51 (600)	44·27 (527·77)	20 (450)	24·91 (428·20)	21 (434)	20·4 (428·6)
6	32	36·33	14	18·05	8	13·9
7	18	30·67	8	13·46	5	9·69
8	28	26·42	3	10·23	5	6·91
9	4	23·14	5	7·91	5	5·01
10	54 (136)	20·50 (137·06)	4 (34)	6·19 (55·84)	6 (29)	3·67 (39·18)
11	3	18·35	7	4·90	4	2·72
12	30	16·58	3	3·90	3	2·03
13	2	15·06	4	3·13	1	1·53
14	2	13·77	2	2·53	1	1·16
15	32 (69)	12·66 (76·42)	1 (17)	2·05 (16·51)	3 (12)	0·88 (8·32)
16	3	—	—	1·67	1	0·67
17	2	—	1	1·37	1	0·52
18	2	—	—	1·13	—	0·40
19	0	—	—	0·93	—	0·31
20	37 (44)	8·79	— (1)	0·78 (5·88)	— (2)	0·24 (2·14)
21	0	—	1	—	1	0·18
22	1	—	—	—	—	0·14
23	0	—	—	—	—	0·11
24	2	—	—	—	—	0·09
25	25 (28)	—	1 (2)	—	— (1)	0·07 (0·59)
	Also at 30 (16), 35 (7), 36, 40 (11), 45 (11), 50 (11), 55 (3), 60 (7), 65 (2), 70 (3), 75 (5), 80 (4), 85 (2), 90 (4), 100 (5), 105, 110, 115, 120 (7), 125 (3), 130, 140, 150 (2), 160 (2), 180 (4), 190, 220, 250, 260, 320, 325, 500, 550		Also at 29, 31 (2), 48, 74 and 97		Also one at 47	
	Total: 15,473 species in 1000 genera		Total: 1671 species in 511 genera		Total: 1251 species in 479 genera	
	$\alpha = 238{\cdot}9$, $x = 0{\cdot}98479$		$\alpha = 250{\cdot}4$, $x = 0{\cdot}8696$		$\alpha = 283{\cdot}8$, $x = 0{\cdot}81509$	

Fig. 23 shows the same data for 171 families of dicotyledonous plants of the world from Rendle (1925). The range for species and genera is much greater. Four families have only a single species, and of course a single genus, while at the other end the Compositae have about 1000 genera and 23,000 species.

It will be seen that the same distribution is found as in the Orthoptera: nearly all families with less than 100 species have α values below 10; with 100–1000 species the indices range from below 1 up to 50; with 1000 to 10,000 species there are few with α below 10 and the upper limit reaches 100; while both families with over 10,000 species have indices over 100.

Again the conclusion is that the larger families have many more genera than would be expected by simple increases in the number of species; and that therefore they differ in structure from the smaller families. On the other hand, there are resemblances and differences which are worth noting. For example, the Piperaceae, with over 1300 species and only 9 genera, have an α value of just over 1, which is almost identical with the Sonnerabiaceae which has only 12 species and 3 genera. On the other hand, the Acanthaceae with just over 2000 species but with 220 genera have an index of 64, which makes a remarkable contrast with the Piperaceae. This point will be discussed later.

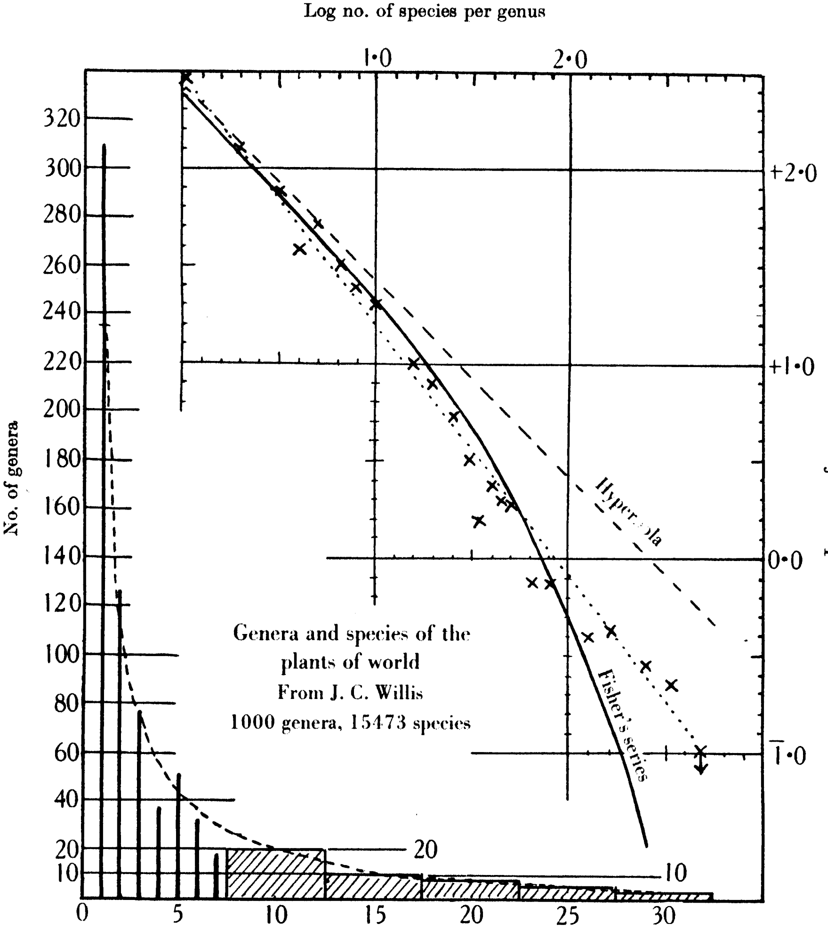


Fig. 18.

As final evidence that the principle applies also to local floras, Fig. 24 shows the results for families of the British flowering plants as given by Bentham & Hooker (1906). Below

10 species per family the error of calculation of α is very high, but again it will be seen that, above this number, the families with more species have higher values for the index of diversity.

Frequency of occurrence of different values of α

Fig. 25 shows diagrammatically the frequency of occurrence of different α values in the dicotyledons of the world (Rendle, 1925). The most frequent value for a family is less

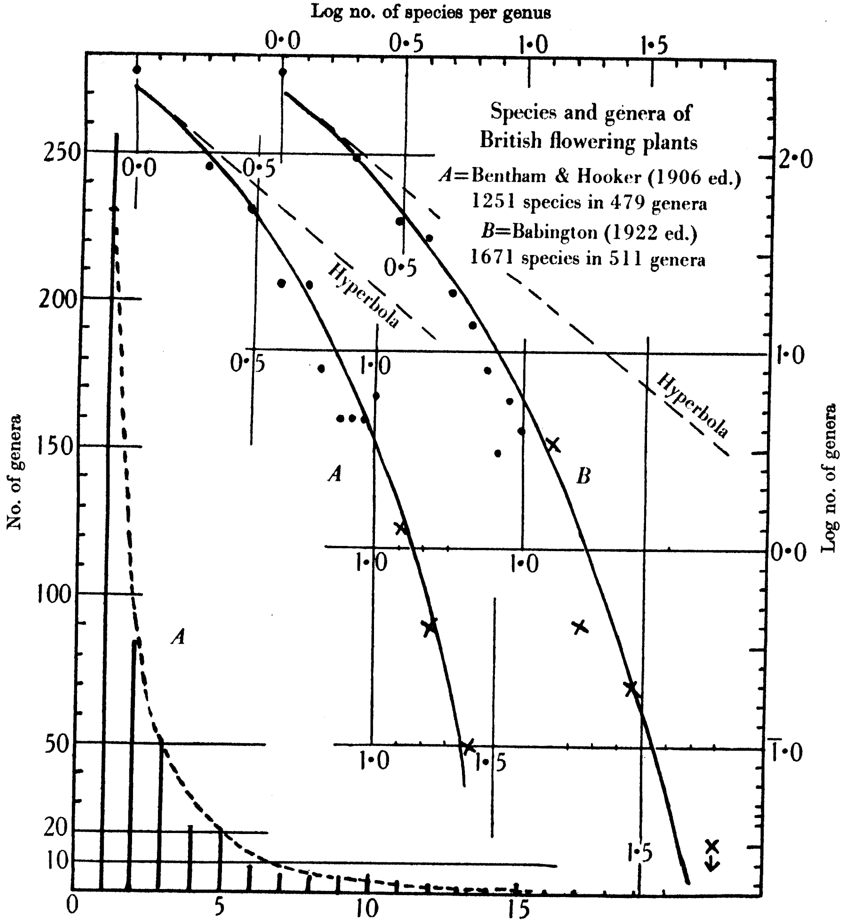


Fig. 19.

than unity; values of 1–2 and 2–3 occur almost equally often, but after that there is a steady fall off. Out of 171 families of dicotyledons, 27 have indices below unity, 22 between 1 and 2, and 23 between 2 and 3.

The α value of all the families together, i.e. of the whole group of dicotyledons, will be the sum of all the values for the different families (see p. 3) and is approximately 1980.

Classification of families of dicotyledons on index of diversity

The problem of the variation in index of diversity in different families appears to be of possible importance in the evolution of the group, as it is only partly explained by the different size of the families.

Other points such as the degree of study of the groups—or the idiosyncrasies of the particular authority who drew up the classification, whether he be a 'splitter' or a 'lumper' will also come in.

Table 16. *Frequency of families of flowering plants with different numbers of genera*

No. of genera per family	Plants of world (Rendle)		British plants (Bentham & Hooker)		British plants (Babington)		Plants of Colorado (Rydberg)	
	Observed	Calculated	Observed	Calculated	Observed	Calculated	Observed	Calculated
1	19	31·08	32	29·3	36	32·55	46	42·88
2	7	15·48	17	13·8	19	15·25	36	20·09
3	14	10·28	9	8·6	13	9·51	7	12·55
4	5	7·67	8	6·1	3	6·68	7	8·82
5	5 (50)	6·11 (70·62)	3 (69)	4·6 (62·4)	4 (75)	5·00 (68·99)	4 (100)	6·61 (90·95)
6	7	5·07	2	3·6	3	3·90	3	5·16
7	4	4·33	1	2·9	1	3·13	3	4·15
8	3	3·77	—	2·4	—	2·57	3	3·40
9	7	3·34	3	2·0	1	2·14	3	2·83
10	5 (26)	2·99 (19·50)	1 (7)	1·7 (12·6)	3 (8)	1·80 (13·54)	— (12)	2·39 (17·93)
11	6	2·70	1	1·4	1	1·53	1	2·04
12	3	2·47	—	1·2	1	1·32	2	1·75
13	3	2·27	1	1·1	1	1·14	—	1·51
14	1	2·10	2	0·92	—	0·99	1	1·32
15	1 (14)	1·95 (11·49)	— (4)	0·81 (5·43)	1 (4)	0·86 (5·84)	— (4)	1·15 (7·77)
16	2	1·83	2	0·71	—	0·76	2	1·01
17	3	1·71	1	0·63	—	0·67	1	0·89
18	5	1·61	2	0·56	5	0·59	1	0·79
19	—	1·52	—	0·50	—	0·52	—	0·70
20	3 (13)	1·44 (8·11)	— (5)	0·44 (2·84)	— (5)	0·47 (3·01)	1 (5)	0·62 (4·02)
21	2	1·36	—	0·40	—	—	1	—
22	4	1·29	—	0·35	—	—	—	—
23	2	1·23	—	0·32	—	—	—	—
24	1	1·18	—	0·29	—	—	—	—
25	2 (11)	1·13 (6·19)	— (0)	0·26 (1·62)	— (0)	—	— (1)	—
	Also at 26, 28, 30 (2), 32 (3), 33, 38, 40 (4), 41 (2), 45 (4), 47, 50 (3), 58, 60 (2), 61, 62, 63, 66, 70 (4), 73, 74, 75, 80 (2), 85, 88, 90, 100 (2), 110, 120, 130, 150, 170 (2), 200, 205, 220, 270, 280, 380, 550, 1000		Also one at 27		Also at 30, 37, 46 and 47		Also at 27 (2), 36, 70 and 80	
	Total: 7452 genera in 172 families		Total: 479 genera in 89 families		Total: 511 genera in 96 families		Total: 682 genera in 127 families	
	$\alpha = 31{\cdot}2$, $x = 0{\cdot}995830$		$\alpha = 31{\cdot}19$, $x = 0{\cdot}93887$		$\alpha = 34{\cdot}76$, $x = 0{\cdot}93631$		$\alpha = 45{\cdot}76$, $x = 0{\cdot}93712$	

To show the differences and to stimulate discussion I have prepared Table 17 which shows all the families of dicotyledons, according to Rendle's classification, grouped according to

(1) the value of the index of diversity,

(2) the number of genera in the family.

Two sets of questions emerge from this table. First, what are the reasons that cause two families to be in the same group? Is it accident, or amount and quality of study, or some question of geographical distribution, or the age of the group in evolution?

Table 17. *Classification of the families of dicotyledonous plants according to value of α and number of genera*

Value of α	No. of genera: 1	2–5	6–10	11–20	21–50	51–100
Less than 1	Tropaeolaceae Callitrichaceae Nepenthaceae Garryaceae Myrtaceae Casuarinaceae Calycanthaceae Hydrostachyaceae Clethraceae Symplocaceae	Hippocastanaceae Aceraceae Balsaminaceae Elatinaceae Salicaceae Hydnoraceae Chloranthaceae Droseraceae Tamaricaceae Agnifoliaceae Meophrastraceae Nolanaceae Lentibulariaceae Plantaginaceae Stylidiaceae	Begoniaceae Fagaceae Piperaceae Ebenaceae			
1		Sarraceniaceae Frankeniaceae Caricaceae Margraviaceae Elaeagnaceae Sonneratiaceae Salvadoraceae Globulariaceae Martyniaceae	Betulaceae Aristolochiaceae Resedaceae Cistaceae Buxaceae Oxalidaceae Polygalaceae Haloragaceae Valerianaceae	Dilleniaceae Geraniaceae		
2			Juglandaceae Magnoliaceae Berberidaceae Nymphaeaceae Linaceae Staphyleaceae Vitaceae Pittosporiaceae Connaraceae Cornaceae Plumbaginaceae Styracaceae Dipsacaceae	Myristicaceae Passifloraceae Loasaceae Burseraceae Polemoniaceae Orobanchaceae Caprifoliaceae Goodeniaceae		
3				Ulmaceae Aizoaceae Violaceae Dipterocarpaceae Crassulaceae Combretaceae		
4			Pyrolaceae	Portulacaceae Ternstroemiaceae	Loranthaceae Cactaceae Primulaceae Oleaceae	

The following eleven Families with less than 10 species are omitted owing to large error in calculating α:

- Julianiaceae
- Cannabinaceae
- Cynomoniaceae
- Sauruaceae
- Ceratophyllaceae
- Bixaceae
- Datiscaeae
- Empetraceae
- Punicaceae
- Hippuridaceae
- Adoxaceae

						No. of genera	
					101–200	201–500	Over 500
5	Rafflesiaceae Diapensiaceae	Ochnaceae Hydrophyllaceae	Ranunculaceae Lythraceae Epacridaceae				
6–7		Balanophoraceae Nyctaginaceae Lecythidaceae	Santalaceae Polygonaceae Papaveraceae Bombacaceae Amonaceae Myrsinaceae Loganiaceae				
8–10	Lardizabalaceae	Hamamelidaceae	Phytolaccaceae Monimiaceae Lauraceae Capparidaceae Guttiferae Zygophyllaceae Podostemonaceae Thymelaeaceae Onagraceae Sapotaceae Convolvulaceae				
11–15			Urticaceae Amarantaceae Tiliaceae Malvaceae Simarubaceae Meliaceae Celastraceae Rhamnaceae Campanulaceae	Moraceae Proteaceae Myrtaceae			
16–20				Caryophyllaceae Annonaceae Sterculiaceae Malpighiaceae Rosaceae Araliaceae Ericaceae Gentianaceae Boraginaceae Solanaceae			
21–50				Chenopodiaceae Menispermaceae Flacourtiaceae Cucurbitaceae Anacardiaceae Saxifragaceae Verbenaceae Gesneriaceae	Rutaceae Sapindaceae Melastomaceae Apocynaceae Labiatae Bignoniaceae	Scrophulariaceae	
51–100					Cruciferae	Acanthaceae Euphorbiaceae Rubiaceae Umbelliferae Asclepiadaceae	
101–200						Leguminosae	
Over 200							**Compositae**

Secondly, why do two families with the same index of diversity have widely differing numbers of genera, or two families with the same number of genera have widely differing values of α? Again much the same questions arise, and I am not botanist enough to contribute greatly to the discussion. I am, however, continuing this line of study with data from different groups of insects.

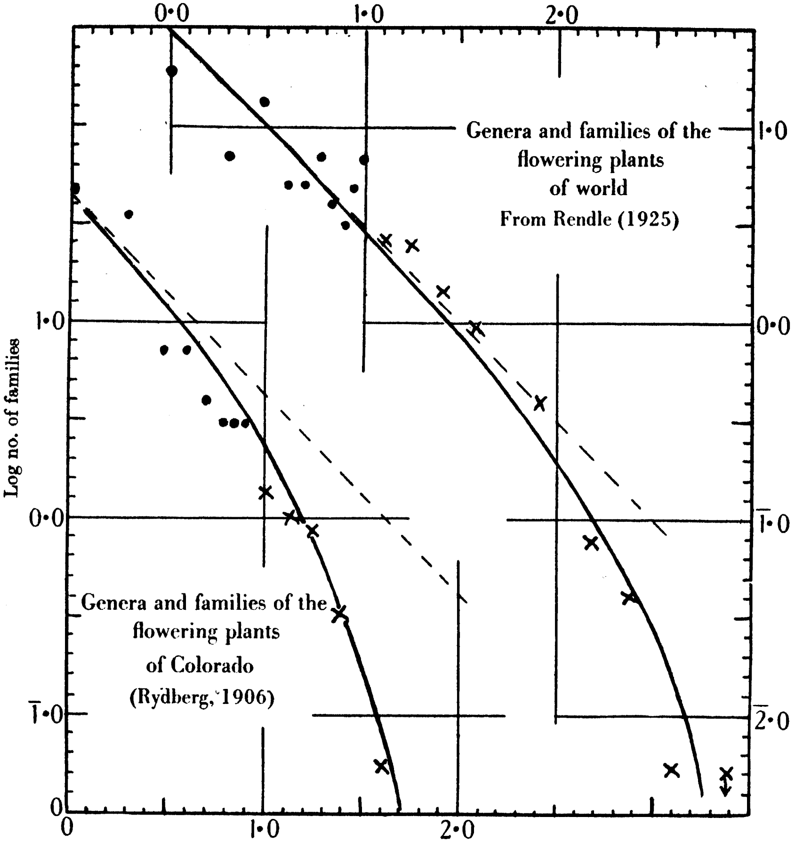


Fig. 20.

5. General discussion

We have in this paper discussed the application of the logarithmic series and the conception of the index of diversity as a measure of the extent to which groups are divided up into units, or units are classified into groups. We have shown that calculations based on this theory give a close fit, and sometimes a remarkably close fit, to observed facts in the frequency distribution of plants in different associations and in samples of different sizes; in the distribution of lice on the heads of their hosts; in the distribution of different species of mosquitoes in American cities; and in the number of butterflies of different species captured in Malaya. In a previous paper (Fisher *et al.* 1943) it has also been shown to apply well to numbers of Lepidoptera and of Capsidae (Heteroptera) caught in a light trap at Harpenden.

All these are problems of the distribution of individuals into groups, and usually into species; and they conform more or less to the original conception of sampling of a mixed population from which Fisher deduced the logarithmic distribution. We have also shown here that the same series explains—or at least will fit well—the frequency of genera with different numbers of species in several different groups of animals and plants, and also the frequency of families or subfamilies with different numbers of genera. The fit of the facts to the logarithmic series is very much closer than to the hyperbolic series previously proposed by several writers.

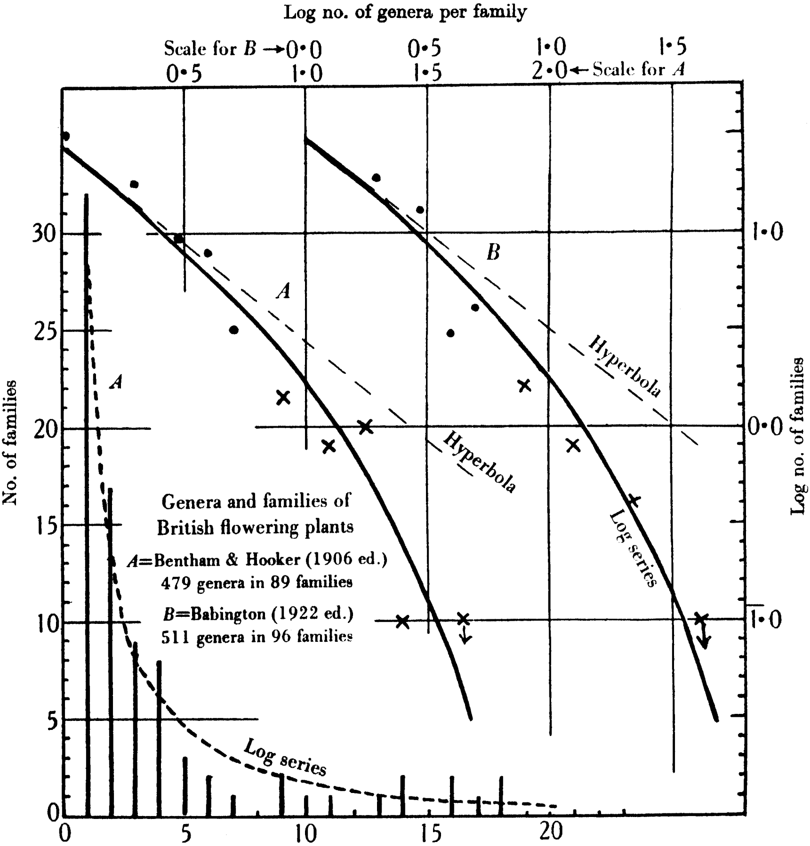


Fig. 21.

If we allow that the close fit is anything more than a series of coincidences we must admit that there is a fundamental law and order in the frequency of species with different numbers of individuals; in the frequency of genera with different numbers of species; and in the frequency of families with different numbers of genera; and further, the law and order must be approximately the same for each.

In my own somewhat limited experience of systematic or taxonomic work on insects, I have always held the opinion that the 'species' of good systematists were about 90% biological realities and 10% groupings of convenience. I have never had the same feeling of confidence in the systematist's 'genera' which I would have classified as perhaps 20% biological reality and 80% personal opinion and convenience. If, however, the grouping of individuals into species, as classified by systematists, is subject to the same mathematical laws as the grouping of species into genera, it seems to imply that the biological reality of genera is of the same order of reality as that of the systematic 'species'. Unless, of course, the logarithmic series is so universal that it can include in its scope the idiosyncrasies of individuals and opinions based on quite insufficient evidence.

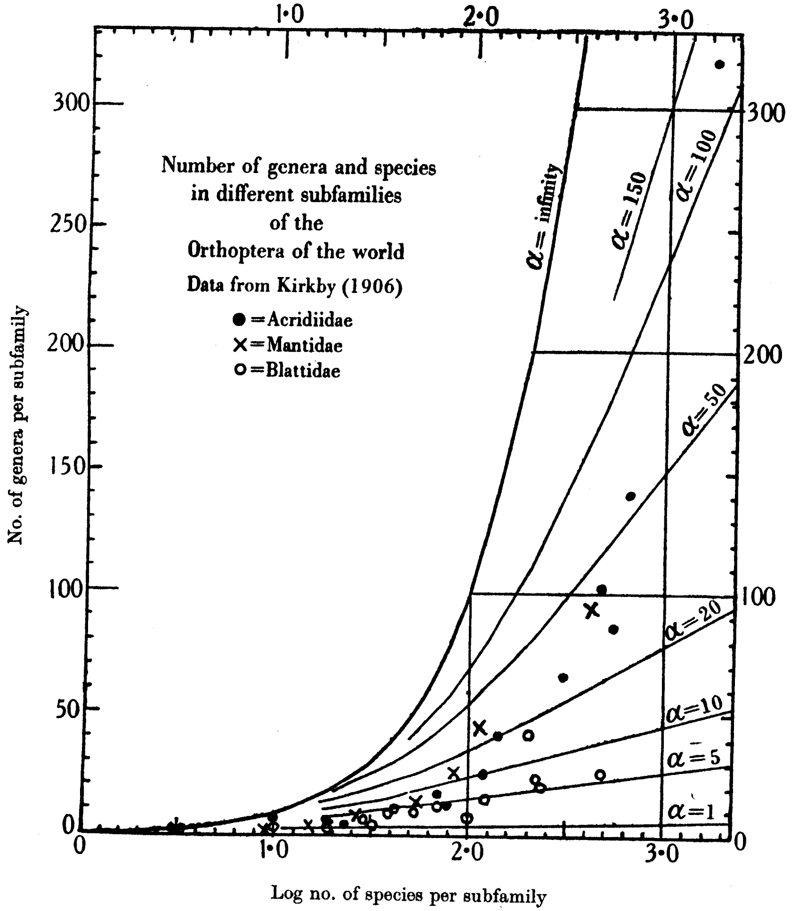


Fig. 22.

It is important, I think, at this stage to distinguish between the real biological species or genus, and the estimate made by the systematist from the material available; much in the same way as the statistician distinguishes the 'parameter', or real truth towards which he is striving from the 'statistic' or estimate of the truth that he determines from his sample. It is also important to note that the logarithmic series gives no information as to whether a systematist is right or wrong in classifying a number of species into many or into a few genera. But once the number of genera has been fixed, we can see immediately if the division has been carried out consistently. One authority may be a 'splitter' and the other a 'lumper' of species or genera; yet both, or neither, may be consistent as tested by the log series.

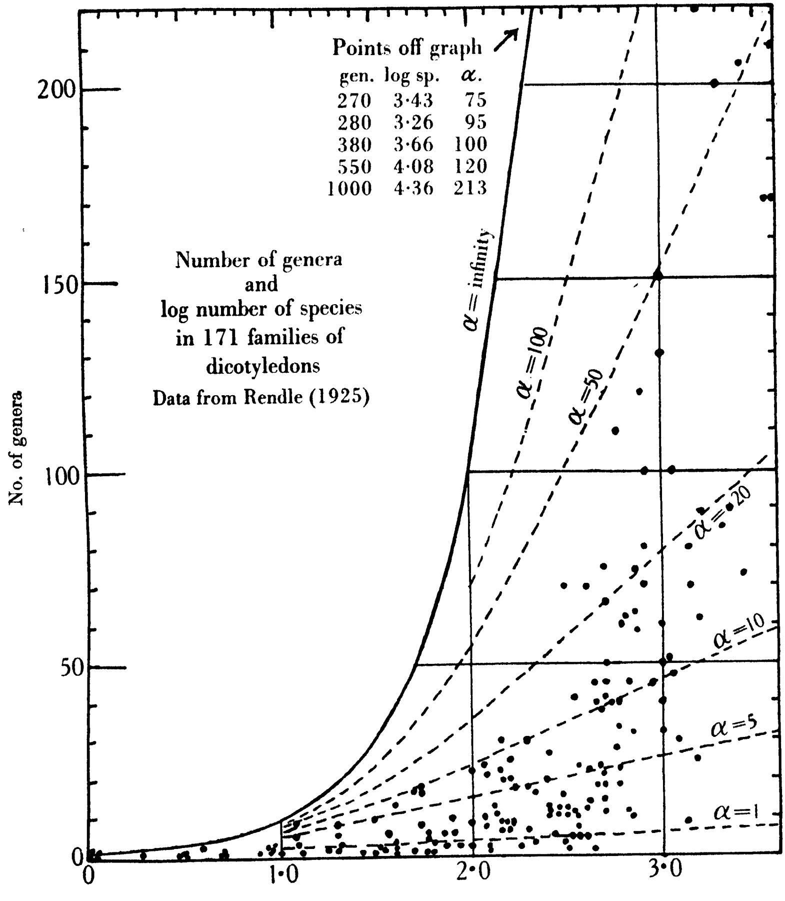


Fig. 23.

In this connexion we should notice how very close indeed to the logarithmic series Kirkby has quite unconsciously come in his classification of some of the families of Orthoptera. The Mantidae are the most remarkable with 805 species classified in 209 genera. This gives the calculated number of genera with one species as 82·27 and the observed 82; the calculated number of genera with 1–5 species as 166·88 and the observed 169; and the calculated number of genera with 6–10 species as 25·98 and the observed 24.

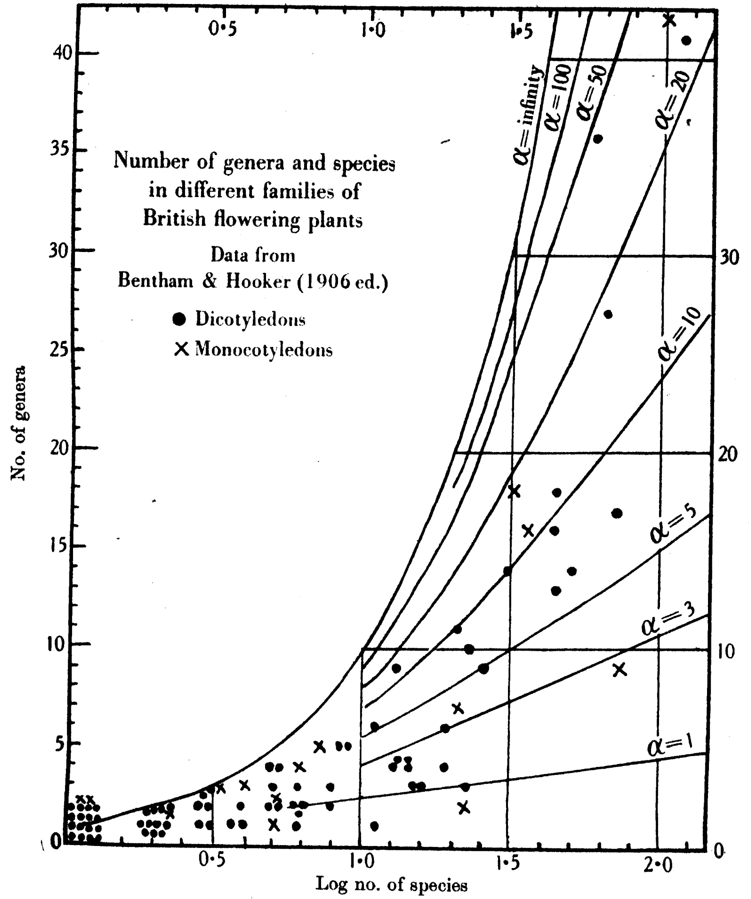

Number of genera and species
in different families of
British flowering plants
Data from
Bentham & Hooker (1906 ed.)
● Dicotyledons
× Monocotyledons
α = infinity
α = 100
α = 50
α = 20
α = 10
α = 5
α = 3
α = 1
No. of genera
0
5
10
15
20
25
30
35
40
0·5
1·0
1·5
2·0
Log no. of species

Fig. 24.

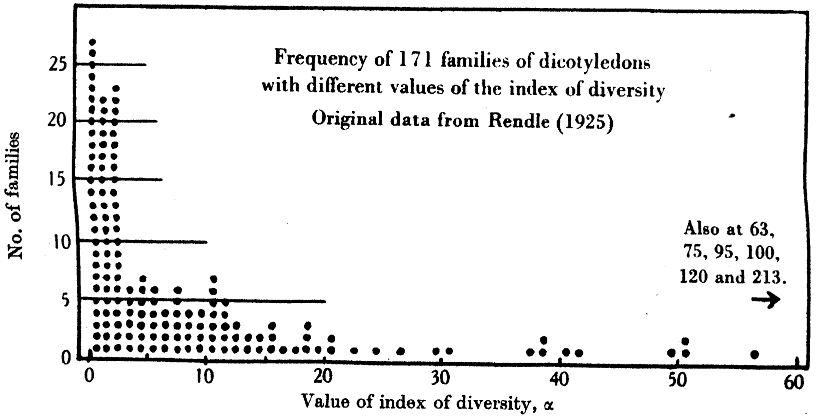

Frequency of 171 families of dicotyledons
with different values of the index of diversity
Original data from Rendle (1925)
Also at 63,
75, 95, 100,
120 and 213.
→
No. of families
0
5
10
15
20
25
0
10
20
30
40
50
60
Value of index of diversity, α

Fig. 25.

It seems to me possible that in a relatively small group revised largely by one man, and particularly in the days when the multiplicity of species (at least in the insects) had not grown beyond its conception as a whole by one brain, the classification is more likely to be psychologically consistent, and hence mathematically consistent, than in a larger group in which many authorities have had their say to different extents in different parts.

In other words, I would suggest that the basic natural classification would be consistent mathematically with some series, such as the one under consideration, and that departures from consistency would be due to errors or incomplete knowledge on the part of the person or persons responsible for the grouping.

In this connexion it is interesting to note how close to the logarithmic series are the numbers of men with different numbers of lice on their heads. This is a purely mechanical problem, with no question of doubt about the identity of either individual lice or individual heads; and with 7442 lice or 461 heads the calculated number of heads with one louse is 107·15 and the observed 106; and the calculated number of heads with 1–10 lice was 303·25 and the observed 304.

There is, however, one general inconsistency that must be noted. In the present paper calculated and observed series are given for 22 sets of data. In only one of them is the observed n_1 definitely below the calculated; in two more it is slightly below; in two almost identical; and in 17 cases the observed n_1 is above the calculated. In the paper on light-trap captures in Harpenden already published (Fisher *et al.* 1943), there were given 27 sets of figures, in 19 of which the observed n_1 was above the calculated and in only 8 below. In some as yet unpublished analyses of light-trap captures of Lepidoptera in U.S.A. I have calculated eleven series of frequency distributions and they all give calculated n_1 below the observed; sometimes the difference is small but in others quite large; in one case the calculated n_1 is 10 and the observed 19.

There seems therefore to be a general tendency for the logarithmic series to underestimate the number of groups with one individual, as compared with the observed facts. Either the theory is incomplete or there is some biased error in the observations producing too many very small groups. In some cases groups with 2, 3 and 4 individuals are also under-estimated, but more usually they give observed results below the calculated so that the figures for groups with 1–5 units are very much nearer than calculated results. In the case of individuals and species it means that there are too many extremely rare species, and this might be partly explained by the fact that in general systematists are more interested in rare species than in common ones and will take more trouble over the description of a 'new species' than over the identification of a second species of one already known.

In the case of species grouped into genera it means that there are too many monotypic genera. This might be partly explained by an unfortunate desire on the part of a systematist to describe new genera, but this would not produce the result if the process of splitting was applied equally to large and to small genera.

There is undoubtedly need for further investigation both by testing of new observations and by further examination of the mathematical theory in the light of the present results.

Turning to the conception of the index of diversity we see that it can be applied with interesting and stimulating results to such problems as the number of species of plants on areas of different sizes, and can be used to give an estimate of the number of individual plants on a given area, which can be used as a check against other deductions. Various writers have suggested empirical formulae connecting the number of species on quadrats of different sizes, and some of them have pointed out the approximate straight-line relationship between the logarithm of the area and the number of species over a part of its range. Fisher's index of diversity is, however, the first theory to give an accurate estimate for both small and large samples, the first to be based on a logical foundation, and the first to link up botanical data on quadrats of various sizes with zoological data on samples containing different numbers of animals. It marks, I think, the beginning of a new mathematical study of mixed populations as opposed to the study of the changes in numbers of a single species—perhaps in relation to one or two parasites—which has occupied the attention of mathematically minded biologists, or biologically minded mathematicians, in recent years.

6. INDEX OF DIVERSITY USED AS A COMPARISON OF DIFFERENT POPULATIONS

It is interesting to note that in addition to the points discussed above in connexion with the index of diversity, this mathematical conception gives up a new possibility in the comparison of the fauna or flora of different areas. If we have two areas of land, say two islands, or two counties or two countries, then according to their ecological and geographical relationships there will be more or fewer species common to the two areas. If the two areas are close together and similar ecologically there will be many species common; but of course, owing to the accident of sampling, there will always be some in each area that do not occur in the other. At the other end of the scale, with complete difference between the two areas there would be no species in common.

Now the index of diversity gives us the possibility of calculating—with certain assumptions and under certain conditions—the number of species that would be common to two areas if they were of the same population only differing in size.

The assumption necessary is that the density of population is the same for both; and as will be seen later the areas must be of different sizes. The mathematical treatment is as follows:

If there are two localities with areas A and B and with a and b species respectively in the group of plants and animals under consideration; then if the two are samples of the same population the value of α will be the same for each, and the same for the two together.

Let x be the theoretical total number of different species found on the two areas together on the supposition of identity. Then

(1) The increase in numbers of species by adding B to A

$$=x-a=\log_e \frac{A+B}{A}.$$

(2) The increase in numbers of species by adding A to B

$$=x-b=\log_e \frac{A+B}{A},$$

hence

$$\frac{x-a}{x-b}=\frac{\log (A+B)/A}{\log (A+B)/B}$$

(whether logs to base e or to base 10 are used). From this x can be calculated and the number of species common to both areas is of course $a+b-x$.

It is interesting to note that the above method only gives x if the two areas are of different sizes. Expressed graphically we are testing the fit of three points to a curve of a particular form; and if two points are identical the method of test fails.

As a practical example we may take the two Channel Islands of Guernsey, 24 square miles, having 804 flowering plants and ferns, and Alderney, 3 square miles, with 519 species (Marquand, 1901).

On the assumption of identity of flora

$$x-804=\alpha \log_e \tfrac{27}{24}=\log_e 1{\cdot}125, \quad x-519=\alpha \log_e \tfrac{27}{3}=\log_e 9{\cdot}00,$$

whence $x=820{\cdot}126$.

Otherwise on the theory of identity of flora there should be 820 species in the two islands combined, or 503 species common to both.

The actual number given in Marquand's *Flora* as common to both is 480 or 95·4 % of the calculated number. This indicates a close degree of relationship.

When, however, the method was tested to see the relationship between Wicken Fen and Scolt Head Island—each with an area just over a square mile and with 185 species of plants—it broke down as explained above, owing to the similarity of the two areas. In fact, the total number of species common to the two, on the assumption of identity is $185-0{\cdot}69\alpha$, and so is dependent on the value of the index of diversity, which cannot be found from the data given. It could, however, be found if we knew the number of species on a definite fraction of either of the two localities. Further work along these lines is now being carried out.

7. SUMMARY

The paper describes the application of a logarithmic series to a number of problems of the division of individuals into species and of species into genera, the range of which is best seen from the table of contents.

The series, first suggested by R. A. Fisher in this connexion, is

$$n_1, \frac{n_1}{2}x, \frac{n_1}{3}x^2, \frac{n_1}{4}x^4, \text{etc.},$$

where n_1 is the number of groups with one unit and x is constant less than unity. Unlike the hyperbolic series, which had previously been considered to apply to some of the cases discussed, the logarithmic series is convergent: both the number of groups (e.g. species) and the number of units (e.g. individuals) can be summed. When several samples are taken from a population containing a number of species it is found that the ratio n_1/x is constant and, as it is therefore a characteristic of the population, it has been called the index of diversity.

The logarithmic series is found to fit extremely well to a large number of frequency series drawn from insects, birds, butterflies and plants, except that there is a slight tendency for the calculated n_1 to be below the observed.

It also fits well, sometimes extremely well, to the number of genera with different numbers of species in standard classifications of groups of both animals and plants.

The conception of the index of diversity is applied to problems of the number of species of plants on different areas, and to the comparison of floras of different areas with interesting results.

A classification is given of the 171 families of dicotyledons according to their index of diversity to stimulate a discussion as to which may be the factors which bring about differences and resemblance in this Index. In general, the families with large numbers of species and of genera have large index of diversity, but there may be a very big range of index in families of approximately the same size.

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NATURE CONSERVATION AND NATURE RESERVES

Report of the Committee appointed by Council on 26 May 1942

Approved by Council, October 1943

Revised Terms of Reference (5 January 1943). To consider and report on the whole question of the conservation of nature in Britain with special reference to plant and animal communities and species, and to draw up a list of areas that should, on ecological grounds, be kept as National Nature Reserves.

CONTENTS

PAGE
Introductory note. The N.R.I.C. Report . 45
1. What is there left to preserve? Vegetation and animal life of Great Britain . 46
2. Aims and objects of nature conservation . 49
3. The social background of nature conservation . 51
4. Methods of nature conservation . 57
  (i) Vegetation . 57
  (ii) Invertebrate communities . 59
  (iii) Fish . 60
  (iv) Amphibia and reptiles . 60
  (v) Birds and mammals . 61
    (*a*) Complexity of the factors at work . 61
    (*b*) Introduced species . 63
    (*c*) Uses of reserves for animals . 64
  (vi) ‘Sanctuaries’ or ‘Species Reserves’ . 64
5. Machinery of nature conservation . 65
  (i) National Nature Reserves . 65
  (ii) ‘Habitat Reserves’ and ‘Species Reserves’ . 66
  (iii) ‘Amenity’ and ‘Educational’ Reserves . 66
  (iv) Local Nature Reserves . 67
  (v) Scheduled areas . 68
  (vi) Administration of Nature Reserves . 70
    (*a*) National Reserves . 70
    (*b*) Local Reserves . 71
6. The need for an educational campaign 73
7. The establishment of a National Wild-Life Service . 74

Summary . 76

General Conclusions . 81

Introductory note. The N.R.I.C. Report

Your Committee have found themselves in some difficulty because of the co-existence of the ‘Nature Reserves Investigation Committee’ with very similar terms of reference. That Committee was appointed in the Summer of 1942, shortly after the appointment of our own Committee, by the Conference on Nature Preservation in Post-War Reconstruction, which was itself formed in 1941, on the invitation of the Society for the Promotion of Nature Reserves, of delegates from societies and other bodies interested in natural history. The Conference held three meetings during 1941 and laid down certain principles concerning nature conservation and the selection, use and maintenance of Nature Reserves (Conference Memorandum No. 1, November 1941). In 1942 Sir William Jowitt, in his capacity as chairman of the Ministerial Committee concerned with problems of reconstruction, invited the Conference to appoint an appropriate Committee which could advise Government on matters relating to Nature Reserves. The Conference forthwith appointed the N.R.I.C.

It will thus be seen that the N.R.I.C. is a quasi-official body, and it has facilities for carrying out its work which are far greater than those available to the British Ecological

Society. Furthermore, the interests of ecology are well represented on the N.R.I.C. by several prominent members of the B.E.S., though they serve as appointees of the Conference, not as directly representing the B.E.S. It might therefore be held that the work of the B.E.S. Committee was unnecessary and redundant. That, however, was not the view taken by our Council, nor by at least two of our members who are also members of the N.R.I.C. It is felt that the interests of ecology as such and the views of ecologists ought to be independently formulated, and that our Society is the proper agency to do this and to draw up a list of areas which should be preserved as of national importance on ecological grounds. But it is also true that the motives for nature preservation which are not specific to ecological science are so mixed with those which are that it becomes misleading to deal with the latter alone and to omit all reference to the former.

The following Report, therefore, while naturally written from the ecological point of view, attempts to argue the case on the widest grounds and to make suggestions in other interests besides those of specialized ecology, more particularly those of enjoyment by the people at large of characteristic British scenery and the educational value of the preservation of wild nature. Considerable use has been made of the memoranda and report[1] of the N.R.I.C.

Two important conclusions which have necessarily affected the work of your Committee have been reached by the N.R.I.C. One is the decision to separate *National Reserves* from *Local Reserves*, the former to represent a minimum of habitats and communities which should be preserved as of national importance and which it is recommended should be acquired outright by the State; while the latter, many of which already exist, would be preserved in other ways by various bodies or persons, including Local Authorities, and administered locally. The other decision is to form local committees, eventually to cover the whole country, for the purpose of obtaining adequate information as to areas it is desired to preserve. The chairman of the B.E.S. Committee independently came to the conclusion that this is the only effective means of obtaining the necessary data. The data obtained directly by the B.E.S. Committee have therefore been sent to the appropriate local sub-Committees of the N.R.I.C. to assist them in their work.

A list of habitats, with their types of vegetation, which should be represented among National Reserves, and a list of suggested National Reserves has been prepared and transmitted to the N.R.I.C. for their information.

The Committee expresses its debt to Mr Charles Elton, Dr H. N. Southern and Dr E. B. Worthington, who supplied valuable memoranda on which the sections dealing with the conservation of animals are mainly based; and to Dr A. S. Watt and Dr A. R. Clapham in regard to Forestry.

1. WHAT IS THERE LEFT TO PRESERVE? VEGETATION AND ANIMAL LIFE OF GREAT BRITAIN

Though the face of Great Britain has been greatly changed by man's work through the centuries, so that most of it is farmland while large parts are now built over, yet there do remain considerable tracts of wild vegetation, much more extensive of course in the wetter climates of the west and the bleaker conditions of the north, where the soils also are on the whole less fertile and less suitable for farming. As the human population has increased in density the populations of larger wild animals have naturally been greatly reduced. Not only have the larger carnivorous mammals been exterminated and the larger predatory birds greatly lessened in numbers, but various other species have decreased or disappeared as suitable habitats became more and more restricted. Nevertheless, the bird population is large, comprising several hundred species, and there are quite a number of small mammals, largely rodents, some of which are too numerous. Of invertebrate animals there are vast numbers of species and individuals belonging to many different groups, though the butterflies and moths are almost the only ones that attract much popular interest.

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[1] *Nature Conservation in Great Britain*: Report by the Nature Reserves Investigation Committee, March 1943.

The wild life of our country is part of our national heritage. Together with and determined by the climate, the physical features and the varied soils, the natural vegetation of the country, with the animals which haunt it, forms the original scene in which our history has unfolded and has largely conditioned the development of our culture and civilization. It has always been and still is a vital source of conscious pleasure and refreshment to large sections of the population, and unconsciously at least it is part of the breath of life of every countryman. To-day it demands our conscious and alert attention, for in the inevitable changes of the next few decades much of what remains will be seriously threatened with destruction or degradation even more rapid than in the recent past. We must preserve what we can of this precious and beautiful heritage, just as we preserve what we can of our ancient buildings and monuments, largely for the same reasons, but also for others.

We cannot of course preserve the whole of what remains. The claims of new building, of agriculture and forestry, must take a prominent place in post-war development. And some animals are too numerous for human welfare. What we can do is to survey the whole problem with careful attention and then take steps to conserve, under proper control, more or less extensive samples of our natural vegetation and so much of our wild animal life as is reasonable and practicable, for our mental refreshment, for the enjoyment of its beauty and interest, and for purposes of study and education.

In considering the problem of conservation we must first deal with the vegetation, because it forms the natural covering of the country and is the ultimate basis, directly or indirectly, of all animal life. When we preserve vegetation we automatically preserve the greater part of the animals which inhabit it, since these are small invertebrates. The larger animals require separate consideration.

The land of Great Britain, especially the lowlands, has been subjected for so long to human occupation and cultivation that little indeed remains in a completely 'natural' state. Apart from the towns and villages, and isolated buildings, the railways, roads, aerodromes, and factory sites, the mines and quarries, most of the lowlands are occupied by farm lands under arable crops or fields of 'permanent' grass. Scattered among these, however, there are woods, and here and there commons covered with heath and wild grasses, largely on soil which did not repay cultivation, at least in earlier times, and used by the 'commoners' for pasture and for the collection of dead wood. As a result of such uses they are often markedly altered from their original condition, though they still bear wild vegetation. On the uplands the picture is different. Cultivation may extend to the height of a thousand feet or more, but above this altitude most of the land is still occupied by natural plant communities. Except at the highest altitudes and in the most remote places the great bulk of the upland country has been used for pasture. Much of it, like many of the lowland commons, is covered with a vegetation of wild grasses and is known as 'hill' or 'rough grazings' largely used for sheep rearing in the great wool industry of past centuries. These include the downlands of the south, much of the uplands of the south-western peninsula, and of the hills and mountains of Wales and the north of England, the Scottish Southern Uplands, and the Highlands. Most of the grassland of these hill grazings owes its present condition largely to the continual nibbling of the sheep. Great tracts of land in the north, however, are not covered by pure grass vegetation, but by heather, bilberry and similar plants, often mixed with grasses, and these moorlands are frequently preserved as deer forest and grouse moor. Much of this land too is covered with bog, or boggy moorland, especially in the very wet climate of the north-west. Above 2000 ft., and especially above 3000 ft., the so-called 'alpine' vegetation begins to appear, and this is little if at all altered by human activity.

Thus the uplands of Great Britain are mainly covered by vegetation which is 'wild', in the sense that the plants composing it are native to the country and have come there by themselves, but nevertheless owes its particular character to human agency, mainly to the constant grazing of sheep and cattle. Vegetation of this kind is spoken of as 'semi-natural'. Much the greater part of the land below 2000 ft. was originally covered by forest or scrub, and this woody vegetation has been removed by felling and clearing to provide fuel and timber for human use, to make room for sheep and cattle grazing, and in the lowlands for agriculture.

Though the lowlands and the lower slopes of the hills were once covered with forest, existing remains of native woodland are very scanty. Not much more than 5% of the land area bore woodland of any sort in 1920, and this included modern plantations. Of the old native deciduous forest, consisting of oak, beech, ash, alder and birch, that which was not cleared was maintained for the supply of timber, small wood, and bark for tanning, though the native timber supply became so scanty several centuries ago that most of the demand had to be increasingly met by importation. Some of this native woodland still remains in a more or less natural condition, and woods dominated by all five of the trees mentioned are represented. Many of these woods have been planted up, mostly on the sites of old woodland, and have assumed most of the characters of natural woodland, though this does not apply to the modern conifer plantations, which introduce quite different conditions. The beechwoods of the southern chalk, the ashwoods of the Derbyshire dales, the oakwoods of the northern and western valley sides, the alderwoods of undrained marsh and fenland, the birchwoods, and the few remaining native pinewoods of the Scottish Highlands, are all genuine representatives of native woodland.

The still undrained marsh and fenlands which remain bear their own characteristic vegetation, but often determined in its detail and distribution by human activity. A very few 'raised bogs' of the kind characteristic of the central Irish plain still survive in the west and north of Britain, and they possess an extremely distinct plant population. The aquatic vegetation inhabiting rivers, lakes, pools and canals is again quite distinct and largely unmodified, though it may of course be destroyed, by man.

Finally, there is the vegetation of the sea coast, of the salt marshes, sand dunes, shingle beaches and sea cliffs. Because it is under the control of the constant and powerful influence of the sea this maritime vegetation, where it has not been destroyed and replaced by artificial constructions, is perhaps least modified by man of all the types, except the fresh-water vegetation and that of the high mountains.

The only way to safeguard and maintain such tracts of this remaining wild country as can and should be preserved is to set aside certain areas and control them more or less closely, according to their nature. Besides the tracts of wild and semi-wild country briefly described above there are a number of man-made habitats which support various animals and plants of great interest to naturalists. Such are the hedgerows of the south and the low stone walls of the north, the embankments and cuttings of railways and roads, the exposed faces of disused quarries, and so on. Some of them, for example hedgerows, are threatened by ill-judged and hasty measures against pests, and though some destruction of these habitats may be necessary, careful consideration of all its implications is wanted before widespread action is taken.

Before we deal with the methods and details of control, it is necessary to consider the various objects of the efforts at preservation.

2. Aims and objects of nature conservation

The first object of nature preservation on a large scale, and the aim which naturally and rightly meets with the most widespread interest and support, is the maintenance for enjoyment by the people at large of the beauty and interest of characteristic British scenery. This depends at least as much upon the vegetation by which the landscape is covered as on its physical features. To preserve unspoiled and free from the chances of 'development', which wholly destroys its character and charm, as much as possible of this landscape is a duty we owe to our descendants, just as obligatory as the duty of securing conditions which will tend to their economic prosperity. As the National Parks Committee wrote in their *Report* (1931), this characteristic scenery is 'of peculiar interest to the nation as a whole—typical stretches of coastline, mountainous regions, moor and downs, river banks and fen. These areas constitute an important national asset, and the nation cannot afford to take any risk that they will be destroyed or subjected to disorderly development.' Under existing conditions destructive changes are possible at any time and place as a result of the activities of the speculative builder, of the establishment of new factories or other industrial or public works, of mining and quarrying, and also, though in a different way, of the activity of the Forestry Commission.

In the age of large private estates, which frequently included beautiful scenery, destructive development was often effectively prevented by the pride of owners in their possessions and their frequent refusal to part with or lease their land even when this would have been extremely profitable. Access to beautiful estates was often, however, refused in order to maintain privacy or in the interests of game preservation. Both maintenance of a beautiful estate intact and permission for access to it depended in any case on the interests or caprice of the landowner. Now that we are passing into a time when the wealth and power of large landowners will probably be increasingly and drastically curtailed, this precarious safeguard of rural beauty will disappear and public action becomes the only means by which it can be preserved.

It is fully realized of course that building and economic development must continue. We must house our people adequately, we must build new factories and construct public works, and we must maintain and improve our agriculture and increase our supplies of home-grown timber. But in addition we must see that we do not hand down to our successors a defaced and ugly land. In particular cases decisions between rival claims to the use of land may well be difficult. Compromise and give-and-take will be very necessary in the 'country planning' that will have to be undertaken, and not only between different possible economic uses but also between these and the preservation of natural beauty. It is true, of course, that much English rural beauty depends upon the villages and agriculture of the past, and how far it can be maintained with the changed agricultural methods of the present and future remains to be seen. But that is a separate question which does not immediately concern us here. Many British landscapes depend for their charm on the stretches of natural and semi-natural vegetation which still survive—the downs, the heaths and moors, many still unspoiled stretches of sea coast and certain tracts of well-wooded country.

Besides the paramount motive of the preservation of rural beauty there are others which are also of great importance. These may be described as the scientific and the educational, and it is the first of these and by implication the second with which we are mainly concerned in this Report.

Our native species of plants and animals, their distribution, habits and relationships, have long been a major interest of British naturalists, who have been increasingly disturbed by the progressive disappearance of species from many of their old habitats as the advance of urbanization destroyed the natural conditions. But it is the rise in importance of the modern study of ecology that has brought into prominence the seriousness of this threat to our native flora and fauna from the scientific as well as from the aesthetic point of view. Ecologists are not only interested in plant and animal species as such: their subject of study is largely the natural aggregations of species and individuals, or plant and animal 'communities' as they are called, that occur in nature. The preservation of sufficient unspoiled examples of these is an essential condition of their work. Plant and animal communities do not consist wholly or even mainly of specially striking or rare species whose diminution or disappearance is deplored. Plant communities are usually dominated by quite common plants, whose presence in great numbers is characteristic of particular conditions and at the same time helps to determine the presence of the host of other species associated with the dominants in the particular habitat. It is the community, the particular aggregation of species in a natural habitat, including those that are common, which is one of the most important objects of ecological study, and the preservation of sufficient examples of such communities is a primary ecological interest.

Oak, beech and ash trees, heather and bilberry and bog moss are very unlikely to disappear altogether from the country, but their continued existence as species is of very limited use to an ecologist if all the oakwoods, beechwoods and ashwoods, the heather and bilberry moors and the undrained *Sphagnum* bogs are destroyed or so modified that they no longer represent natural plant communities. Here the ecological interest almost exactly coincides with the aim of preserving the characteristic charm of British scenery so far as it depends upon natural vegetation. Our heritage of woodland, down and heath, mountain, moor and wild sea coast not only gives us relaxation and refreshment and the enjoyment of beauty but also indispensable objects of scientific study. There is no conflict between these two interests—one may actually be made to serve the other. For appreciation of the natural beauty of landscape is greatly enhanced by the deeper understanding of it—of its geology, of the natural vegetation which covers it, and of the animals that inhabit it, as well as of the uses to which man has or may put it. And this brings us naturally to the third important object of nature preservation—that of education.

Nature study is now widespread if not universal in the lower forms and classes of our schools, and the modern teaching of geography is largely based on regional survey, which concentrates attention on the home region as a geographical unit that can be studied at first hand. In broad outline ecology is a natural development of both these subjects in all rural districts and in towns from which easy access can be had to the country. Knowledge of the nature and significance of our still unspoiled tracts of wild country should be taught alongside knowledge of the human uses to which the land has been or may be put. Only in this way can we educate our future citizens so that they may come to take a pride in the natural beauty as well as in the economic strength of Britain and to give their support to future developments that are wise and balanced.

The permanent success of the scheme for National Parks will depend on the use which is made of them and on the extent of the interest and enthusiasm that can be aroused. Public support to the necessary degree can only be created by greatly increased knowledge, understanding and appreciation of the natural interest and beauty inherent in scenery and vegetation. Both school and adult education on these lines is necessary, and ecological knowledge in the widest sense must be the basis of it. The formation of 'nature reserves' in which scientific work on natural and semi-natural plant communities and their accompanying animals can be carried on will not only advance an important branch of biological science which can be applied to the management and control of a considerable fraction of the natural resources of the country (for ecological knowledge and ecological methods are, and will be increasingly, used in forestry and certain branches of agriculture), but may also be made to contribute, in ways indicated later, to the success of National Parks through the development of public knowledge and appreciation.

Thus the various aims and objects of nature preservation, widely different as they appear to be, are in reality very closely linked. The values involved are first of all those which are now commonly, though most inadequately, described as 'amenity' values. These are perhaps the most important of all, since they touch the deepest sources of mental and spiritual refreshment, both conscious and unconscious, and of these the specifically aesthetic value is really a part. Then there are the scientific, the educational, and indirectly the economic values, and each, as we have seen, reinforces the others. The case for extensive, carefully and scientifically planned, nature preservation thus becomes extremely strong.

3. THE SOCIAL BACKGROUND OF NATURE CONSERVATION

The whole problem of nature conservation requires to be viewed against the human or social background.

The greatly increased pressure of the human population on the native flora and fauna is due not only to increase of population, but also to the much quicker and deeper penetration of modern means of transport. Comparatively remote places are now visited by many more people, who unwittingly, and often through mere numbers, tend to deface their beauty and destroy them as habitats for the native plants and animals. Increased mechanical and chemical means of destruction bear hardly on both plants and animals. The higher vertebrates suffer severely from shooting, trapping, netting, poisoning, and now gassing. This, of course, is intentional destruction, but active forces of destruction require active measures of conservation. Just what should be destroyed and what preserved must become a question of public policy. Ultimately a sound conservation policy must be based on an ecological expression of the resultants of different desires which are often in conflict.

In its general aspect the problem appears as that of resolving a fundamental conflict between conservation on the one hand and development in its widest sense on the other. Greater development of the country's natural resources is inevitable if Britain is to retain her position among the leading nations of the world: at the same time a national scheme of conservation becomes an urgent necessity if we are not to hand down to our descendants a land hopelessly impoverished in a most precious part of its heritage. This conflict is not merely one between rival interests. Conservation is not a sectional interest. Its importance to the community as a whole is comparable with that of development and is inextricably knitted up with efficient development. The ecologist who advocates it can do so in full consciousness of his membership of the whole community and as part of his special duty towards it.

There are many forms of development and their relations to the problem of conservation vary greatly. In the first place there is the building of new towns and villages or extensions to those already in existence; the erection of new factories, power plants, dams, locks, harbours, quays and so forth; the provision of new roads and railways, of new aerodromes and sports grounds. The relevant problems of planning and siting have been discussed in the Scott Report and your Committee would wish to support the recommendations there made for responsible and sympathetic control.

Of wider and more immediate significance to your Committee is the utilization of land for agriculture and forestry.

The land of Great Britain, so far as it is not used for housing the population and for industrial purposes in the widest sense, is mainly devoted to agriculture. Excluding the rough grazings of the hillside grasslands and moorlands, which bear 'wild' vegetation, about two-thirds of the area of England and Wales and about a quarter of Scotland was agricultural land in 1938 (*Agricultural Statistics*, 1938). Woodland of all kinds, on the other hand, only occupied a little more than one-twentieth of the land surface. The great increase of agriculture during the war has been mainly represented by the conversion of 'permanent grassland' to arable, though some areas of heath and hill grazings, as well as semi-wild fenland, have been ploughed. Most of this 'permanent grass' was former arable land that had been 'laid down to grass', i.e., sown with grass seed, or had been allowed to 'tumble down' to grass by pasturing derelict arable land which became colonized by grasses. All such land formed part of the agricultural system, and what has happened is a change in the balance of that system, so that for the most part the creation of new arable does not represent a destruction of wild vegetation. It is unlikely that the total arable area will be further increased to any great extent because the limits of existing land that would repay cultivation have nearly been reached. We must, it is true, make an exception of the 'improvement' of hill pasture by ploughing, manuring, and sowing with clovers and improved strains of grasses, as advocated by Sir George Stapledon. This involves great changes in the composition of the herbage of existing rough grazings which have never been ploughed or manured, are composed of entirely wild vegetation, and cover a very great proportion of the hillsides of the north and west of Britain. The existing areas of hill pasture are so large, however, that a considerable number are likely to escape such treatment and should still be available for ecological work. Furthermore the 'improvement' of hill pasture scarcely alters the scenic character of the landscape. Yet the ecologist must keep in mind the extent of the changes brought about in this way and must secure the conservation of sufficient areas of the more natural hill vegetation for his adequate understanding of the problems which the new agriculture will raise, and of the results of the large-scale experiments which the new methods will constitute. Such understanding will form a large part of his claim to act as an expert adviser in agricultural planning.

The plans of the Forestry Commission for the afforestation of Britain are of very great importance to the ecologist. Our native woodlands are of special and unique interest to him because they represent the final and highest type of natural vegetation over much of the country. At present woodlands, including all plantations, only cover about 5·5 % of the total land area; and these, apart from a few tiny fragments, have been greatly modified by past treatment. The native woodlands are of deciduous trees, chiefly of oak, beech, ash, birch and alder, except in certain areas of the Highlands where the native Scots pine still persists. The replacement of this deciduous woodland by plantations of exotic conifers, or even of Scots pine in parts of the country where it is no longer native, involves a more profound alteration of a smaller remnant of native vegetation than does the activity of the improving agriculturist. The changes in the landscape brought about by such replanting and by the planting of former rough hill grazings with conifers are also much more conspicuous than those due to agricultural improvement. Finally the large-scale experiments undertaken by the forester are expensive and of long duration. While they are of great interest to the ecologist, providing him with much new material and many new problems, he cannot but feel deeply concerned about their careful planning, since errors or failures will be difficult to rectify.

For these reasons your Committee feel strongly that they have a special responsibility to express their views on the relations between afforestation and nature conservation in some detail. They are further encouraged by the fact that the Forestry Commission has recognized the special interests of ecologists in its activities, has promised to give sympathetic consideration to their requests for the conservation of certain areas of existing woodland and has invited co-operation in tackling the problems of afforesting difficult sites.

Given its primary task of producing the kind of timber needed by the nation it cannot be denied that the Commission is bound to plan the formation of extensive plantations of exotic conifers. By far the chief commercial demand (about 94 %) is for coniferous timber; and the areas, poor or useless for arable agriculture, on which most of the new planting has been done, are chiefly areas on which conifers seem to thrive much bette than do the native deciduous trees. But young coniferous plantations, straight-edged, their trees neat in form and precisely aligned, their floors bare of the familiar woodland herbs, undoubtedly introduce into the landscape an alien feature which offends eyes accustomed to the luxuriant irregular beauty of an old native wood. And the offence is deepened where a familiar open hillside has its contours blanketed under masses of dark and sombre foliage. The feeling readily arises that these plantations constitute a deadly threat, not only to the old beauty of the countryside into which they intrude, but also to its wild life, both animals and plants. Nor are these fears unfounded. The flora and fauna of coniferous woods are very different from those of our deciduous woods. Some of the characteristic species of coniferous woods are natives of the country and might quickly reach new plantations on open ground. Others, not natives, might gradually establish themselves through the chances of migration and transport. Many of the native species formerly living in the area would certainly be ousted, though some would probably persist. The flora and fauna of old deciduous woods replanted with conifers would certainly be profoundly changed.

It is necessary however to consider a matter which touches deep emotions so strongly with the greatest possible objectivity. The programme outlined in the recent White Paper on 'A Post-War Forest Policy' envisages the planting of 3,000,000 acres of open ground, chiefly rough hill pasture, out of a total existing area of over 16,000,000 acres of rough grazings. This would result rather in the introduction of greater variety into our landscapes than a wholesale destruction of their beauty, even if, as is likely, the greater part of 2,000,000 acres of existing woodland are also replanted with conifers—provided always that a substantial amount of native deciduous woodland is maintained. The plantations will lose much of their repellent uniformity and ecological poverty as they grow older. An old plantation of stately, well-grown larch or Scots pine with a ground flora of bracken, bilberry or blue moorgrass has great beauty, though of a different kind from that of an oak or beechwood, and this should be true also of an old plantation of Douglas fir or Sitka spruce. The management of such plantations on silvicultural systems which do not involve clear felling, such as the 'selection system', or, where the practical disadvantages of this are too great, one of the varieties of 'shelterwood', and which permit of self regeneration where viable seed is produced, is highly desirable both aesthetically and ecologically. It is still doubtful how far the productivity of pure coniferous woodland can be maintained in this country, at least on certain soils which show progressive deterioration as the result of the accumulation of coniferous humus, and it may turn out that mixed plantations of conifers and deciduous trees have a wide future in British forestry. The ecology of such mixed woods would be of great interest and thorough investigation of the soil problems involved is much needed.

The expert knowledge upon which such decisions should be based depends on real understanding of the ecological problems involved. This is the most vital consideration, not only for the ecologist but also for the forester himself and for the whole community. Comparison of a coniferous plantation or a mixed crop of coniferous and deciduous trees with a nearby natural wood of native trees is an indispensable step in the acquisition of such knowledge. The interests of the most ardent lover of our English and Scottish landscapes, of the most devoted naturalist, and of the most commercially minded forester, alike demand that there shall be conservation of as large an area as possible of our surviving native deciduous woodland. This should be well distributed over the country so as to include the widest possible variety of sites and of woodland types. Some might well be managed as exploited woods, others should be left quite untouched. In dealing with deciduous woods which are maintained as such it is most desirable, wherever possible, to secure self-regeneration, and this could probably be done in many cases by taking suitable measures, especially by excluding or reducing the numbers of animals which destroy seedling trees. An increase of predators, especially birds of prey, as suggested in Section 4 (v) of this Report, would keep down the destructive small rodents and would both protect the young trees, making regeneration easier, and establish a more varied and interesting wild animal life.

The Southern English climate, especially on the loam and clay soils, is essentially a climate of deciduous woodland, which is a characteristic feature of the landscape whose loss would be a major disaster. Much of it is now in a deplorable condition, partly owing to long neglect and partly to the intensive exploitation of war time. A great deal of this must be replanted, whether with deciduous trees or conifers, but some could be rescued and improved by appropriate measures.

The principal natural forest types, examples of which should be maintained, are the different varieties of beech and oakwood of the south, the durmast oakwoods on siliceous soils and the ashwoods on limestone soils of the west and north, and the remnants of oak, birch and pine wood in the Scottish Highlands. It is pleasing to be able to record that the Forestry Commission has already set aside two areas of old woodland, one in the High Meadow Woods by the banks of the Wye, the other in the New Forest. These will be left completely undisturbed as permanent forest reserves. Thus it is evident that the Commission is prepared to play a leading part not only in timber production but in nature conservation and the progress of ecological knowledge, and we should like to see the closest co-operation between all these interests.

Your Committee feel that the Forestry Commission ought to have a broader mandate now that its practical control of much the greater part of British woodland is being contemplated. There are many ways in which a largely increased forest area administered by a central authority would touch the life of the people as a whole. Among these are the relation of forests to water supply, to erosion by wind and water, to the provision of shelter for man, his crops and stock, to the conservation of wild life, and the general contribution of forests to scenic beauty and amenity. We should like to see the Commission concern itself actively with all these things, by close co-operation with other interested bodies and by the exercise of wider powers. The British people are not, at present, 'forest-minded', but they might be increasingly made so by suitable educational propaganda, and there is no reason why they should not become proud of the national forests as an integral part of rural Britain. Such a broadening of the official outlook would awaken a sympathetic response in quarters at present lukewarm, or even hostile, to plantations seen only as crops of trees for the production of timber. In a word, if British forestry is to play a really worthy part in national reconstruction its aims should be much wider than the meeting of a national need for increased timber supply and the provision of a sound long-term 3 % investment.

Your Committee would wish then to emphasize the common interests of the forester, the ecologist and the naturalist, to welcome their increasing collaboration and to urge that it should be carried further still. They appreciate the strength of the economic pressure which compels the Forestry Commission to plant conifers more extensively than our native deciduous trees. They ask, however, that silvicultural systems other than clear felling should be practised as widely as possible, and that areas entirely composed of native trees should be planted wherever it is economically reasonable to do so. Finally they recommend very strongly the conservation of considerable areas of existing natural woodland as indispensable material for highly relevant scientific investigation, as well as for the other more immediately obvious reasons to which reference has been made.

Another important field of conflict is seen in the activities incidental to game preservation. Game preservation, it has been truly said, is the only form of wild-life management with any history or tradition in Britain. Its object is to protect certain selected animals (almost all of which are birds), so that later on they may be killed for sport. They must be provided with suitable habitats and their enemies must be destroyed. This line of action has had two opposite effects on wild life. Preserving the suitable habitats of game often means preserving considerable tracts of natural or semi-natural vegetation with the animals that inhabit them, so far as these are not hostile to the game itself. On the other hand, the carnivorous birds and animals which prey upon game are ruthlessly destroyed, resulting in a very great decrease in the populations of predatorial species. This in its turn has led to a great increase of small rodents—mice and voles, rats and rabbits—which are a principal food of the predators—with resulting serious and widespread damage to agricultural crops and seedling trees. One conspicuous predator—the fox—is protected, though not without some friction between the hunting and the shooting interests, where these are separate. The status of several of the animals involved is considered in Section 4 (v). Another effect of game preservation on a large scale is the high local density of certain species of game, including ground game, which press hardly on agriculture and silviculture. Not only the pheasants and rabbits of the lowlands, but the large populations of red deer in the highlands do much damage to crops, and the latter to trees. Again excessive density may result in serious epidemic disease, e.g. grouse disease.

It is, however, only just to recognize the important effects of game preservation in the maintenance of natural habitats, not only extensive heaths and moors for grouse and deer in the west and north, but also the deciduous woods and copses used as pheasant preserves and fox coverts which are the habitats of many of our wild flowers and small birds. If game preservation were to cease entirely and no other form of protection put in its place, the whole countryside being devoted solely to the economic interests of agriculture and silviculture, we should lose at once the great majority of our still-existing wild-life habitats.

It would seem that the shooting and hunting interests should submit to a certain curtailment of the privileges they have enjoyed in the past, but it is difficult to envisage a Britain in which this kind of sport was wholly suppressed. If sportsmen would tolerate an increase of predators, would raise fewer pheasants, and be content with a lower density of foxes, grouse and red deer in those regions where they are now excessively abundant, considerable progress could be made towards a juster balance of nature.

Love of the countryside, including its wilder aspects, has certainly not decreased in the population at large during the present century. Indeed, it has been fostered by the freer range of townsfolk through the country made possible by motor transport. Besides the thoughtless people who tend to deface it there are many who earnestly desire to see its natural beauty and interest preserved. Among the more special interests the love of wild birds has increased enormously, as is shown by the work of the Royal Society for the Protection of Birds, which has been active in securing legislation. A recent writer has remarked that the British birds are 'perhaps the most written of...listened to, protected, loved birds in the world'. Their few 'tens of millions have a public not many times smaller in numbers than themselves'. This widespread and intense sentiment can no more be ignored than the Englishman's love of sport, and both must be balanced against purely economic interests. No greater mistake can be made than to minimize the importance of sentiment, to seek to brush it aside as rather a shameful weakness. Sentiment, like other human qualities, can be unduly exalted and misused, but it remains one of the most important and inescapable of human motives, and must be given its just place in social organization.

All such factors as those which have been discussed must be taken into consideration and given their due weight before a sound conservation policy, or any comprehensive planning of land utilization can be devised. The claims of agriculture should come first—that is common ground—but by far the greatest advance here is to be made by improving the cultivation and management of land already used as arable or pasture rather than by bringing extensive new areas into the agricultural regime. The claims of forestry in the proper management of existing woodland and the establishment of extensive new forest areas may perhaps be regarded as coming only second to those of agriculture in national importance. They can be met with all reasonable regard to nature conservation, sport and public amenity if only wide vision and careful broad-scale planning are adopted. This is all-important in the development or conservation of such land as still remains in a wild or semi-wild state. Ecological knowledge, already existing, or accessible to properly directed research, is the essential foundation of any scientific handling of the problems involved. Both the social, the economic, and the ecological facts are indispensable data, and none can be neglected if successful solutions are to be found.

4. METHODS OF NATURE CONSERVATION

(i) *Vegetation*

The indispensable general method of preserving wild plant life together with the small animals which accompany it is to set aside certain areas in which destruction and disturbance can be prevented. This method is not however adequate for the larger birds and mammals, which have to be considered separately (see Subsection (v)).

It has long been proposed to establish a number of *National Parks*, rights in which would be acquired by the State primarily for the enjoyment of the public, in parts of the country famous for the beauty of their scenery, and this proposal will almost certainly be carried out. Such parks will automatically preserve considerable areas of wild vegetation. But National Parks alone will by no means cover the whole of the requirements. In the first place there will be too few of them, and secondly they cannot be managed with primary regard to scientific needs. These require the maintenance of many areas quite unsuitable for the formation of a National Park and very widely scattered through the country.

In addition to the National Parks it is proposed in the N.R.I.C. Report (pars. 15, 16) that a number of large *Scheduled Areas* should be established, and that in these 'development' should be restricted, so that within such areas the main features of natural beauty would not be destroyed, and much natural vegetation would be preserved.

But for purposes of scientific work it is necessary to preserve a considerable number of areas which are generally much smaller, chosen because they represent natural habitats bearing single or several plant communities, and these may be specifically called *Nature Reserves*. Some of the Nature Reserves would naturally fall within the boundaries of the National Parks and Scheduled Areas, but others would lie outside them, and all would require a different type of management from the National Parks.

It has been proposed by the N.R.I.C. that Nature Reserves should be divided into two categories—*National Nature Reserves* and *Local Nature Reserves*. The former, it is suggested, should be acquired by the State, supported from national funds, and administered under a State Authority. Together they should represent all the important British types of natural habitat and natural plant community. Local Reserves, on the other hand, would be acquired or held locally under various arrangements with their present owners, and local, including local educational, authorities would be represented on their governing bodies. The Local Reserves would supplement the necessarily restricted number of National Reserves and could be used for a variety of purposes, scientific, educational and 'amenity', according to their nature and the conditions of their tenure.

In considering the actual administration of Nature Reserves it is essential to recognize, first of all, that informed and careful management is in fact necessary for nearly all reserves as well as for National Parks. A great deal of the vegetation which it is desired to preserve is partly the result of human activity through the centuries. In other words it is 'semi-natural' and not wholly 'natural' in the sense of being the product of 'Nature' alone. This is true for example of downland, of the hillside grasslands and many of the moors of the north and west, of much heathland, of undrained or partially drained fenland, and of most of our deciduous woodland, whether the trees have been planted or not. These types of country together make up by far the greater portion of the regions of which relatively large samples should be preserved. In order to maintain any area of this semi-natural vegetation more or less in its present condition the existing human activities (grazing, burning, mowing, coppicing or selective felling) must generally be continued. This applies to the strictest nature reserve or sanctuary as much as it does to any area to be established as a National Park. If the human activities cease the vegetation immediately begins to change. The formerly grazed downland, the periodically burned heath, the fen which was regularly mown, becomes colonized by shrubs and often by trees. When the human activities cease, the character of the area is wholly altered, and the plant communities with their characteristic animals, which it was desired to preserve, disappear. If coppicing is discontinued in a wood of the 'coppice-with-standards' type, the shrubs become 'overgrown' and the ground vegetation is seriously impoverished owing to the dense shade created. Thus if you 'let Nature alone' in such areas you frustrate the very aim you have in view. With the changes in the plant communities which she immediately initiates the conditions of life are altered and the interesting or rare species which depended for their existence on the former (man-made) environment may disappear altogether.

Areas in which human activity was abandoned some time before reservation show all stages of these changes, the nature and exact course of which are vital subjects of ecological study. For this reason such areas should in general be left to develop their own natural vegetation, and the same is true of certain parts of all newly reserved areas, which should remain undisturbed while most of the reserve is kept in the 'semi-natural' condition that was produced and maintained by human agency. Thus, most of the old-established fen reserve at Wicken in Cambridgeshire is kept as 'sedge fen' or 'litter fen' by clearing invading bushes and periodical mowing, which are essential to preserve for naturalists the fen plants and animals, while small portions are allowed to grow up to the scrubwood community called 'carr'. The same procedure, *mutatis mutandis*, should be adopted in downland or heath regions, where grazing or burning should be continued, except in certain selected portions in which shrub and tree colonization should be allowed. Where it is impossible or undesirable to continue the previous regime, some alternative procedure having a similar effect must be adopted. For example, colonization of heathland by trees, which has been constantly checked or prevented by periodic fires, may also be stopped by uprooting the tree seedlings or saplings.

Areas which have always been free or almost free from human interference are relatively few, but naturally of great ecological importance. They include parts of the sea coast where new soils are accumulating, a considerable number of ponds, lakes and rivers and their margins, and high mountainous regions. In such places we see new plant communities in process of development, and their continued freedom from interference is of first importance to ecologists. They are also of high value because they represent the fragments of really 'wild' nature still existing within the country. Reserves of this nature require much less 'management' than the 'semi-natural' areas which owe their character partly to the continued activity of man.

It will be clear from what has been said that for the great majority of reserves expert management is essential if they are to fulfil their purpose, and this is true alike of National Parks and of both National and Local Nature Reserves. Any nation-wide scheme of reservation must provide for such administration, and it is ecological knowledge combined with practical experience of land management which is necessary.

If a series of National Parks is established by the State, a primary aim must be to preserve the beauty of the scenery they include. This cannot be done unless the natural vegetation is substantially maintained, for the beauty of most scenery depends at least as much on vegetation as on the physical features which it covers. A great deal of the ecological knowledge required has been gained during the past quarter century, and this is being steadily increased as new studies are undertaken. Here we have the natural source not only of the technical management of Nature Reserves, but also of the technical advice needed for preserving the character of National Parks. It is proposed by the N.R.I.C. that there should be separate authorities for National Parks and National Nature Reserves, and this would probably be a sound arrangement because the problems involved in the administration of the two are in several respects different, but the function of ecologists in advising on those problems which depend on the maintenance of natural vegetation in the parks cannot be ignored. Further work on the protected reserves will continually throw fresh light on such problems and increase the weight of the advice that can be given on the treatment of areas of similar nature within the National Parks.

(ii) *Invertebrate communities*

It is not generally realized what an enormous proportion of the total fauna, both in numbers of species and in numbers of individuals, is contributed by the invertebrate groups, nor how few of these, outside those groups (such as butterflies, moths, beetles and snails) which attract the collector, are known to, or are even seen by, the average naturalist. Nevertheless, after plants, they constitute the most important element in the preservation of any population in its natural balance; nor in many cases could the plants themselves subsist without the ubiquitous activities of these animals. The extreme complexity of their specific interrelations, their vital effects upon the soil, their attacks upon the plant elements, from the minute fungi and algae to the largest trees, both as direct feeders and disease carriers, and their essential place in the food chain in providing food and as predators themselves, set problems of the highest scientific and economic importance. Fortunately, the great majority of these communities and species are automatically protected by the preservation of the type of vegetation in which they find their natural habitat, and little more need be done beyond maintaining the existing plant balance and securing that the breeding stocks of the few more showy rare species are not reduced below the danger point by the depredations of collectors.

Because of these facts and their economic implications it is a prime need to secure the preservation of a sufficiently representative series of invertebrate communities so that their intricate relations can be closely studied in the balanced state which they have achieved under particular representative conditions. The preservation of areas which include representative plant communities will, to a large extent, achieve this object; but there will be other areas—particularly perhaps among semi-natural and man-made habitats—where preservation should be based upon the existence of important invertebrate populations and species.

(iii) *Fish*

Angling is so widespread a sport, appealing to such large numbers of the public, that the conservation of fish has behind it a really powerful interest. Practically all fresh waters are regularly fished, and the anglers, often through their clubs and associations, backed by the fishery boards, are probably strong enough to see that fresh-water fish populations are not seriously reduced.

The pollution of rivers and streams, both by industrial effluents and by sewage, is by far the greatest factor inimical to fish. A good deal has already been done to reduce this evil, but more general and stringent measures should be taken. Conservation of particular lakes, rivers and streams is probably unnecessary for the preservation of fish, as such, though there are many ponds and small lakes which ought to be reserved, with surrounding land, in order to preserve the plant life and accompanying animals—water birds and others. Such action will, however, often reduce the free water available for fish and thus work against the angling interest: it may in fact ruin the water from the point of view of the fisherman. This conflict can be resolved in some cases by appropriate management, providing for periodical partial clearing of vegetation, in other cases by abandoning the attempt to preserve the fishing as well as the vegetation and the other animals. Taking a wide view, the relinquishment of angling in a limited number of fresh waters will not seriously restrict the opportunities of fishermen.

There are, it is true, a few very local species of fish, such as char and species of *Coregonus* in some lakes, but these are not, on the whole, much sought after by anglers, and there is no serious danger of their numbers being reduced.

The adoption of more effective means of preventing the pollution of fresh waters, such as the setting up of Regional Boards, based on catchment areas and responsible for all matters pertaining to the purification of sewage, industrial effluents and polluting storm water, as recommended by the Pure Rivers Society, is by far the most important measure that can be taken for the conservation of fish and the other aquatic animals and plants essential to their existence.

(iv) *Amphibia and reptiles*

Most of the twelve native species belonging to these two groups are of widespread distribution in the country and in no particular danger, but a few are local and need protection. Of these the natterjack toad is confined to sandy areas, both coastal dunes and inland. Its occurrence on certain dunes, such as those of the Lancashire coast, furnishes part of the case for reserving such areas. The edible frog is not a native, but has been introduced to certain places in the past and may still survive in some areas. If so, it might well be preserved as an interesting form which is not known to be seriously inimical to native species.

The smooth snake is a very interesting species apparently confined to the New Forest and sandy areas in neighbouring counties. It is a harmless snake feeding chiefly on sand lizards, slow-worms and small mammals. The sand lizard is another interesting species with a discontinuous restricted range, occurring both in the same region as the smooth snake and also on the Lancashire dunes.

The distribution of these two reptiles and the natterjack toad therefore form one good reason among many others for forming reserves (probably National Reserves) in both these regions.

(v) *Birds and mammals*

Different considerations apply to conservation of the higher vertebrates, the warm-blooded birds and mammals, partly because of their great powers of movement and partly because certain kinds directly involve human interests. These animals cannot be conserved simply by a passive policy of setting apart particular land areas as reserves, though this is necessary to protect certain breeding stocks.

The problem always eventually becomes one of attaining and preserving a certain density and distribution of the population of the species concerned in different parts of the country. This involves positive and active management which cannot be planned and carried out without knowledge gained by research and application of the results of research to the field problem. It is useless to attempt to preserve a sample of the animal population as one preserves a library, museum or ancient monument. Carefully calculated methods of conservation and control are even more necessary here than in the management of reserved tracts of wild vegetation.

Even in the United States with its huge wild life parks the passive policy of simply making such reserves, however large, has often conspicuously failed adequately to protect wide-ranging species such as migratory birds; and elk (wapiti) have been systematically shot by 'sportsmen' at their points of passage into and out of the parks.

(*a*) *Complexity of the factors at work*

Besides the special research and active management required to control each species the proper balancing of various material and cultural claims is necessary as a preliminary to a decision as to the precise aims of control. Adequate publicity and the promotion of public knowledge and interest by education are also required to obtain a secure foundation in popular support for the measures taken, just as they are for the proper support and use of National Parks.

The sectional interests involved give rise, as we have seen, to very different human attitudes towards different kinds of animals. Perhaps the most conspicuous instance, already discussed in general terms, is the attitude of shooting men to different species according to whether they are suitable objects of sport or whether, on the other hand, they prey on those objects. Thus shooting men wish to increase the populations of the native black game, woodcock, red grouse, common partridge, and the introduced French partridge and pheasant, while they want to see diminished or wiped out the native populations of sparrowhawk, magpie, carrion crow, stoat, weasel, red fox, polecat, hedgehog, as well as the introduced little owl, grey squirrel, brown rat and domestic cat—or at least the 'hunting cats' of the countryside. Since there are shooting rights over probably 80% of our farmland, excluding the large areas of hill grassland, the dominance of the shooting interest has led to a great scarcity of predators following upon the perfection of modern small arms and efficient 'game-keeping'. The fox is an exception because much as the shooting man dislikes the animal the hunting man insists on its preservation. Some sort of compromise has been arrived at between the two interests—the less difficult because the same people often pursue both sports.

The rabbit was introduced to this country a very long time ago, and the variations of its status in public estimation through the centuries and at the present day, afford an excellent example of the conflict of interests. At first rabbits were apparently scarce and fetched relatively high prices, but by the fifteenth century they may well have been as abundant as they are now judging by the numbers provided at certain feasts, and in the sixteenth century Gesner describes the 'copia ingens cuniculorum' in England. In the seventeenth century rabbits were highly valued as a source of food and fur, and so they have remained until quite recent years. In Scotland they were little known until the nineteenth century, when they rapidly increased so that they are now almost as abundant and ubiquitous as in England, except at high altitudes. They occur in great numbers on almost every island and islet round the Scottish coast, apparently always introduced by man, according to available records. At the present day the rabbit is valued by the sporting farmer, by the large landowner who preserves them in 'warrens' for rough shooting, by the fox-hunt which sometimes 'farms' them as food for foxes, by the professional trapper, by the hatmaker, by the poulterer and his customers, and by the poaching villager who likes to be able to trap or shoot an occasional rabbit to supplement his meagre larder. Most naturalists would be sorry to see rabbits disappear completely, and many members of the public find them very attractive animals. The progressive forester, farmer and market gardener, on the other hand, naturally regard rabbits simply as pests, and indeed in their pre-war numbers they did very serious damage to crops in certain districts, besides completely ruining great tracts of rough grazings. The overwhelming motive of conserving all foodstuffs in wartime has swept away opposition, and rabbit 'control', which in this case means wholesale extermination, has been established over large parts of the country. Nevertheless, there is a case for allowing the continued existence of a moderate rabbit population in some areas.

The war upon predators has resulted in a great increase in the number of small rodents—the mice and voles—and these do a great deal of damage to young plantations, besides having had a decisive effect in preventing the natural regeneration of our deciduous woods by eating off the seedling trees. The common vole multiplies excessively in young forest plantations which are often grown on hillsides open to walkers and naturalists as 'National Forest Parks' established by the Forestry Commission. In high density the voles damage young trees very severely, but in low density damage is rare. The presence of voles modifies the dominant grass vegetation and allows a number of flowers to become conspicuous, thus providing a more varied and attractive vegetation. The voles also bring to the hills an impressive fauna of predators such as buzzard, kestrel, long-eared and short-eared owls, which cannot live comfortably in areas where game is intensively preserved. By checking the growth of the strong coarse grasses, such as purple moor-grass (*Molinia*), which is often dominant on the damp western and northern hillsides, and by their constant burrowing, which aerates the soil, a moderate population of voles would probably actually benefit the growth of the young trees. Thus there is a strong case for maintaining such a population at a moderately low density.

Many more instances could be given of the complex tangle of motives, feelings, interests, habits and activities which affect the density and distribution of our higher vertebrate fauna, but two or three will suffice. The red squirrel is very widely regarded as a charming animal whose disappearance would be deeply regretted, but it certainly does shattering damage to conifers by ring-barking in the crown. The American grey squirrel, introduced on a ducal estate because of its attractiveness, has spread over wide areas and is certainly a more serious pest in plantations, especially of maturing conifers, than the red squirrel, for whose widespread decrease it is probably largely responsible. On more than one Hebridean island visiting biologists have collected so many individuals of endemic races of mice as to endanger their existence, though they are of the highest interest to naturalists. Cornish fishermen would like the seals exterminated, believing that they endanger the supply of fish. Scientific surveys suggest that this is a mistaken view, though complete proof has not yet been obtained. The presence of seals adds a strikingly attractive feature to our coastal scenery.

In the post-war planning of agriculture, a wide range of policies has been advocated and amongst these it is proposed that hedgerows and small copses should be largely eliminated. Hedgerows, it is held, compete with the adjoining crop, may harbour injurious pests and weeds, and at the same time hold up the intensive mechanization of farming which is most effectively carried out in large fields. Such a policy if applied to extensive areas would largely destroy the beauty of much of the English lowlands. It would destroy the main habitats of many of our most cherished wild flowers and also the breeding places of most of our small birds. Moreover, though the breeding of injurious insects might be reduced by the abolition of hedgerows, in the opinion of many ornithologists the consequent drastic diminution of small birds would remove one of the most important checks on the insect pests of farm and fruit crops. Finally hedgerows provide shelter for farm stock and are essential as wind breaks for many crops. The removal of hedgerows and the filling in of the associated ditches may bring about on the lighter soils erosion both by wind and water. This is an example of the complexity of the problems and interests concerned when a policy seeks to change on a large scale the biological and agricultural balance of the countryside.

(*b*) *Introduced species*

At various times different landowners have introduced to their estates, for the sake of amenity or sport, a great variety of exotic animals, including Siberian roedeer, Japanese deer, Chinese waterdeer, wallaby, fat dormouse, and grey squirrel; among birds, little owl, Canada goose, bobwhite quail; among Amphibia and reptiles, edible frogs and Mediterranean green lizards; among fish, rainbow trout, sunfish and black bass. Fur farmers have introduced silver and arctic fox, muskrat, nutria, and mink. The three last named have escaped and spread, muskrat with seriously destructive results, though it has now been exterminated. The interest of some people in the new and the bizarre is often stronger than in familiar native species, and the introducers probably gave no thought to the effects of the strangers on our native animals, or on other interests than their own, effects which are sometimes very serious. It is suggested that the introduction of exotic species should be forbidden except under special licence.

(c) Uses of reserves for animals

The use of a reserve for any particular species of animal is closely dependent on the size and movement of the animal in question and on the vulnerability of its breeding population. In Britain the main use of special reserves for vertebrates would be to protect (*a*) breeding stock, at vulnerable periods of aggregation (herons in 'heronries', gannet, shearwater, grey seal, etc.), (*b*) roosting aggregations of bats, and (*c*) very local species such as bearded tit, crested tit and bittern, including endemic island races of small mammals. Such reserves would form convenient places for long-term scientific work. On the other hand, many birds and the larger mammals are constantly passing from one area where they may be protected to another where they may be destroyed. Accurate knowledge of the habits of each species, which can only be obtained by research, is essential before effective measures of control[1] can be devised. The mere establishment of a reserve in which alone an animal is safeguarded is not sufficient.

(vi) '*Sanctuaries*' *or* '*Species Reserves*'

The word 'sanctuary' is often applied to areas reserved in order to protect rare or specially interesting species of animals or plants which are in danger of becoming rare. This is a highly desirable object, and it should be possible to protect a large proportion of such species by choosing for reservation at least some of the areas in which they naturally occur. Certain rare mammals and birds can only be effectively protected by safeguarding their breeding places and forbidding their destruction over considerable areas of wild country such as might be chosen as National Parks or Scheduled Areas, or over the country as a whole. Rare plants and rare invertebrates are much more narrowly localized and could often be safely included in comparatively small reserves.

The term 'sanctuary' was deliberately avoided by the N.R.I.C. in their report because its use sometimes implies a disastrous policy of 'letting nature alone'. Enclosing a reserve containing rare species while neglecting to maintain the conditions which enabled those species to exist and flourish results in changes which often lead to their disappearance. The processes referred to on p. 14 have free scope and the 'sanctuary' becomes a wilderness of the hardiest and most aggressive plants and animals. It may even become a mere 'focus of weeds and vermin' in the vigorous words of one critic. For this reason the N.R.I.C. use the term 'species reserve' instead of 'sanctuary'.

The desire to save rare species from complete extinction, in order to prevent the permanent impoverishment of our fauna and flora which their disappearance would mean, is very widespread. It is felt by naturalists who are not ecologists, by ecologists themselves, and by many 'lay' members of the public. A distinct 'kind' of animal or plant is a natural focus of interest. It must always be so, since species are the fundamental units of our flora and fauna, and it is of aggregations of the individuals of particular species that plant and animal communities are made. Furthermore, the fact that a particular rare species is a natural member of a particular community is always of ecological interest, and the ecology, i.e. the conditions of existence, of a rare species may be of great significance. Hence the ecologist would always like to see rare species protected in the ways suggested, though rare species, as such, are not his *primary* interest, which is the study of species, whether rare or common, and of the communities which they form, in their natural habitats. For this reason ecologists could not possibly be content with limiting reserves to 'sanctuaries' for the preservation of rare species. To be effective a 'sanctuary' or 'species reserve' must be a sample of the particular community in which the rare species finds a natural home, and to preserve that species the community in which it lives, its proper habitat, must be preserved. The stress is therefore to be laid on preserving the community: if the samples preserved contain rare species their interest is increased, but the choice of reserves cannot be limited on that ground.

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[1] The word 'control' is here used in its proper sense of 'regulation', not as synonymous with destruction, a sense in which it is now often misused.

Some ecologists hold that it is of little use to try to preserve species which have been so persecuted that the breeding population has been reduced below the critical limit and recovery is unlikely. The kite, of which a few pairs only are said to remain in Wales, is given as an instance. The decline of a species owing to persecution must, it is argued, be arrested at an earlier stage if efforts to preserve it are to be effective. It is probable, however, that the strong sentimental urge to try to prevent a species which has become rare from disappearing altogether will always lead to an attempt to preserve the last remnants of its breeding stock in the hope that it may recover. It is important to remember that it is protection of the breeding stock and its habitat which matters. It is of little use to forbid the destruction of stray individuals.

5. MACHINERY OF NATURE CONSERVATION

We have now considered the main problems involved in nature conservation and the kinds of method necessary for their successful solution. It remains to deal with the machinery that must be set up if those methods are to be applied with effect, and we must first consider the methods of establishing nature reserves.

Hitherto such reserves as exist have for the most part been given by their owners or bought by public subscription and vested in bodies like the National Trust or the Society for the Promotion of Nature Reserves. A certain number belong to local bodies or trusts of various kinds, and some remain in the possession of private owners who have expressed the intention of keeping them as reserves, with the further intention, in certain instances, that they should ultimately pass into the hands of some body which would maintain them in perpetuity. It is clear that if any considerable part of our remaining wild life is to be conserved these haphazard methods are not enough, valuable as they have been in the past, and that some comprehensive and systematic plan must be adopted. In regard to conservation by the establishment of reserves the Nature Reserves Investigation Committee has taken the first important step by proposing a primary distinction, already referred to, between National and Local Nature Reserves.

(i) *National Nature Reserves*

'The...purpose...of ensuring the survival of natural and semi-natural communities of plants and animals to provide material for serious studies can be met only by means of reserves in districts suitable to the particular wild life to be preserved; and the reserve must be managed in these interests and not with any other object. Their distribution bears no relation to arbitrary boundaries or centres of population, and their selection and conservation must be based on a single plan for Great Britain as a whole. Their management must be subjected to a unified direction with full responsibility at the centre...if their characteristic features are to be preserved, a continuing expert control must be established. Reserves of this kind are a national concern and will for convenience be referred to as National Reserves.'[1]

The kind of Reserve made for the purposes described in the passage quoted is called elsewhere in the N.R.I.C. Report a 'Habitat Reserve', and it is, in effect, a community or ecological reserve. The purposes described are those with which your Committee is primarily concerned. The proposal to establish a series of National Habitat Reserves under 'continuing expert control' and 'subjected to a unified direction with full responsibility at the centre', is one which has the complete agreement and support of your Committee.

The National Nature Reserves should include relatively large areas and embrace the set of successional plant communities characteristic of a particular type of natural habitat, e.g. down pasture, chalk scrub and yewwood, and beechwood, on the chalk downs. In some cases it would be possible and very desirable to include within one reserve two or more commonly adjacent types of habitat, e.g. saltmarsh, sand dune and shingle beach.

Large habitat reserves would serve as excellent sites for long-term ecological research both on plants and animals.

(ii) '*Habitat Reserves*' *and* '*Species Reserves*'

Besides the Habitat Reserves the N.R.I.C. would distinguish 'Species', 'Amenity' and 'Educational' Reserves. The Species Reserves are intended to secure the survival of rare or very local species. Some of these would also come under central control as National Reserves. The term 'Species Reserve' was adopted by the N.R.I.C. in place of 'Sanctuary', as has been already explained, because of the unfortunate implications which the latter term sometimes carries. But the N.R.I.C. realize that there is no real scientific distinction between Habitat and Species Reserves since they state that 'Species Reserves must in fact be a special kind of Habitat Reserve, in that a species cannot be preserved in natural conditions apart from the communities within which it is able to thrive' (N.R.I.C. Report, par. 18 (ii)). Since this is undoubtedly true, it would seem that if a certain number of Habitat or Community Reserves were selected because they not only represent good examples of plant and animal communities but also because they contain rare or local species, as would be desired by all naturalists, that would meet the case. The regime of management would not differ, since it is the community containing the rare species which has to be maintained. We regard the statement that 'Species Reserves will usually be of smaller size than Habitat Reserves' (par. 18 (ii)) as rather dangerous. For example, supposing a rare species is confined, say, to 2 acres within a particular more extensive habitat or community, it would be a mistake to confine the reservation to that area alone, even with a marginal safety zone. Narrowly localized species sometimes spread from their original area, and they may abandon it altogether and move to a neighbouring one: if only the area actually inhabited by the species at a particular time were reserved there would be no opportunity for such a move. It is always the type of habitat containing the species that it is important to safeguard.

(iii) '*Amenity*' *and* '*Educational*' *Reserves*

It is not contemplated by the N.R.I.C. that Amenity and Educational Reserves should be National Reserves, since these 'subserve local rather than national needs' (par. 21 (ii)).

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[1] *Report of N.R.I.C.*, 'Nature Conservation in Great Britain', par. 7.

Presumably 'national amenities' are considered to be sufficiently supplied by the National Parks, 'National Forest Parks', and 'Scheduled Areas' (see pp. 24–6 of this Report). The N.R.I.C. Report (par. 15) calls attention, however, to the fact that many Scheduled Areas 'could be made to fulfil within themselves and by the simplest means all the three purposes of nature conservation', i.e. scientific studies, enjoyment of nature, and education in natural history. We regard it as important to stress the point that most, though not quite all, Nature Reserves, whether national or local, can likewise fulfil all these functions, and that it is most desirable that they should be made to do so. In this way they will be of the greatest use to the widest range of interests and will therefore obtain the largest measure of public support. There is no reason whatever why the public should not be allowed free access to a self-regenerating beechwood for instance, or any other type of natural or semi-natural wood, provided that they can be successfully deterred from damaging it, and there is every reason why it should be used for teaching students, both children and adults, some elementary lessons in natural history. Such woods are of primary interest and value to the ecologist as examples of important native types of vegetation with their naturally accompanying animals: many of them are of great and characteristic beauty, and they can all be used to notable advantage in education. The same may be said of many other types of habitat in which reserves should be established, such as downland and heath, sand dune, moor and mountain. It is only in a few cases, where the vegetation is easily destroyed or damaged by trampling, or rare species of birds or plants have to be protected, or scientific experiments are in progress, that public access would have to be restricted and regulated.

The conclusion seems to be that *all* Nature Reserves are really 'habitat reserves', that the maintenance of their value, scientific, aesthetic or educational, depends essentially on their proper management and that this must be ecologically instructed. The detailed regulations governing access and use must vary considerably according to the nature of the particular reserve, and only a competent management can properly decide what can be permitted and what should be forbidden in each.

(iv) *Local Nature Reserves*

'These would comprise areas the preservation of which is of local rather than of national importance.' 'They would be owned and managed by societies, local authorities or individuals' (N.R.I.C. Report, par. 21 (ii)). Habitat, Species, Amenity, and Educational Reserves are all contemplated in the N.R.I.C. Report under the category of Local Reserves. There are of course a considerable number of such reserves now in existence, and they serve very various purposes. Many belong to the National Trust, and most if not all of these have been vested in the Trust with the object of securing to the public the use and enjoyment of areas of natural beauty. They would fall under the N.R.I.C. class of 'Amenity Reserves'. Some of them, however, such as Wicken Fen in Cambridgeshire, are in fact of greater scientific than 'amenity' value; others, such as Scolt Head and Blakeney Point on the north coast of Norfolk, are of great value from both points of view; and all of them, so far as they include natural and semi-natural vegetation, have some ecological value. The objects of the National Trust do not include nature conservation for scientific purposes, though in fact the existence and activity of the Trust have been instrumental in preserving areas which can be and some of which are actually used for such purposes. This is possible because the Trust properties are administered by local committees, and on some of these the 'natural history' interest is strongly represented, so that permission is freely given to qualified people to carry on scientific work within the Trust area. Though the Trust could hardly be so reconstituted as to fulfil the scientific functions of the authority responsible for *National* Nature Reserves, it would be of advantage to the formation of *Local* Reserves if it could add to its objects of preserving places 'of historic interest and natural beauty' by including 'scientific interest'. On important archaeological sites the scientific and the historical (or prehistorical) interests merge.

The Society for the Promotion of Nature Reserves has, on the other hand, the primary object of preserving areas of natural history interest and holds a few reserves acquired on this ground. These also are administered by local committees and in some of them ecological work has been carried out.

Both the National Trust and the Society for the Promotion of Nature Reserves are organizations of national scope, but many, probably the majority, of their properties, on account of their nature or of their geographical position, are mainly of local use, though visitors from a distance may not be infrequent. The N.R.I.C. would probably wish to class the bulk of these properties as Local Reserves. There are also other local reserves scattered through the country, intended for one, or more than one, of the purposes described, and with the ownership vested in local authorities, local societies, trustees, or private individuals.

Local reservation of areas for all the purposes discussed will undoubtedly continue to be made whether a national scheme of reservation is adopted or not, and since the reservations will usually be due largely to local effort the ownership and administration of such reserves must naturally be determined by local wishes. As in the case of National Reserves it seems unnecessary to divide such reserves into rigid categories, since they can so often be well employed for more than one purpose, and where possible it is highly desirable that the different functions should be carried on side by side. In this way and under enlightened management, the various interests can be harmonized, and a wider understanding of all can be developed. In certain cases, such for example as areas reserved for the scientific interests of naturalists and in fact presenting little opportunity for enjoyment by the public at large, the reserve must be kept for scientific purposes if these are to be effectively pursued: in other cases part of a reserve can be set aside for ecological observation, ecological experiment or educational purposes, while the rest is left to the unrestricted use of the public. By means of demonstrations of ecological work it should not be impossible to interest many members of the public in this activity, and in the intimate bearing it has on the proper maintenance of the whole area, to the advantage of all concerned. The opportunities for a widened nature study by school classes are very obvious.

The important point is that there is no real conflict of different interests in the conservation of nature. Each can, and should, help the others, and all that is required to bring about harmony and co-operation is an understanding of the facts and principles involved.

(v) *Scheduled Areas*

'These areas were defined in Conference Memorandum No. 1 (p. 2) as "areas in which further development would be prohibited or drastically restricted. In these the existing movement of the public would in no way be interfered with"...any question of acquiring the land or interfering with its present usage or ownership would not arise. The only requisite for the preservation of their natural interest and amenity value is that they should be protected as far as possible from destructive changes' (N.R.I.C. Report, par. 14).

'If such areas were carefully selected, many could be made to fulfil within themselves and by the simplest means all the three purposes of nature conservation...and they would certainly secure in a most satisfactory manner the preservation of many types of plant and animal community of the greatest importance for the advancement of scientific or economic studies. These areas would vary greatly in shape and size. The method might for instance be satisfactorily applied to saving some of the as yet undeveloped parts of the coast-line and such areas as the Norfolk Broads. Other sites which might be so chosen contain villages and even small towns and are extensively cultivated. Here it would be necessary to impose some restriction, or at least a carefully planned control, on further building and perhaps in other ways' (par. 15).

'It is suggested that such areas should be zoned in the relevant Planning Scheme for protection as Rural Zones or sometimes as "Private Open Spaces" or in some other instances as "Agricultural Land".'

'There are many areas of land in rural districts, containing communities of flora and fauna of scientific interest, which it may be felt unnecessary to acquire as nature reserves, so long as the land is adequately protected from development. If any such land is scheduled under the most suitable of the categories indicated it will be safe, unless and until the Planning Authority subsequently make an Order, with the approval of the Ministry, declaring the land no longer reserved....Where areas have been scheduled in Planning Schemes for preservation...with the object of protecting their scientific interest, no subsequent Order varying the use of such land should be made except with the consent of, or at least in consultation with, the National Reserves Authority' (par. 50).

Your Committee is in cordial agreement with these proposals. If an adequate number of well-selected areas can be scheduled in this way, so much of rural Britain will be safeguarded as can reasonably be preserved in the face of other imperative national requirements. The outstanding purpose that will be served is the maintenance of a large part of our national heritage of beauty, both that which depends on natural landscape and vegetation and that which owes its character to the rural settlement and agriculture of the past. Incidentally, as it were, many sites of great interest to the ecologist will be preserved, whether they are made specific Nature Reserves or not.

The scheduling of extensive areas will require great care if on the one hand large samples of the most important and characteristic tracts of country are to be preserved and on the other hand existing legitimate interests are not to be unduly interfered with. Much will depend on the ultimate Government decision as to the conditions of land ownership, and on the issue of the conflict between purely economic interests and the imponderable but vitally important value of preserving the country from defacement. Apart from areas scheduled for the sake of maintaining a mainly agricultural countryside, there are five main types of country in the regions east and south of the midlands which depend for their character largely on natural and semi-natural vegetation and are of the greatest importance. First, there are the still unspoiled parts of the coastline, including sand dunes and shingle beaches, salt marshes, cliffs and undercliffs. The importance of these is widely recognized. Secondly, there is the chalk country with its downland pasture, scrub and woodland, including the characteristic and specially beautiful beechwoods.

There should be at least one scheduled area on the South Downs, one on the North Downs, at least one on the western chalk area (Hants, Wilts, Dorset and Berks) and one on the Chiltern Hills. Thirdly, there is the heathland, some of it of little or no value to agriculture, but unfortunately, from the point of view of rural preservation, very suitable for new building estates. Several areas including wide stretches of heath should be scheduled—in East Anglia, in the south-eastern counties, and in Dorset. Fourthly, there are the extensive tracts of country on clays and loams, as in the Weald, which support many deciduous woods, largely oakwoods in 'coppice with standards', alternating with man-made grassland. Fifthly, there is the area of the Norfolk Broads, which includes the only remaining considerable area of unspoiled fenland in Britain. The total square mileage of this fenland is not large, since it is confined to the comparatively narrow river valleys of the Bure, Yare and Waveney and their small tributaries, but it is of unique importance both for public amenity and for ecological interest. Thousands of people annually find pleasure and healthy exercise in sailing, rowing and fishing on the broads and rivers, and the adjoining unspoiled fenland forms a large part of the natural background of their enjoyment. The undrained or partly drained fenland, with the aquatic flora and fauna of the broads and rivers themselves, is of the highest interest to ecologists, and there are many problems connected with it awaiting ecological investigation, besides many local species that should be preserved. Some of the natural woods of alder, birch and other trees and shrubs that have sprung up on parts of these fens are among the very few practically virgin woods remaining in Britain. If it cannot be made a National Park, this whole fenland area should at least be scheduled against destructive changes, and there should be one or more National Nature Reserves established within it.

In the west and north of the country there are many areas of importance, and the choice is much larger, for there is a much greater extent of uncultivated land. There are, however, some areas of outstanding importance which will doubtless receive attention from the local subcommittees of the N.R.I.C.

(vi) *Administration of Nature Reserves*

(*a*) *National Reserves*

Under this head, as we have seen, the N.R.I.C. would recognize only Habitat and Species Reserves, and they would wish to see established a central National Reserves Authority 'having equal and parallel status within its own field with that of the National Parks Authority', which, it is assumed, would control the National Parks (par. 32). 'The necessity for a single central body with full executive responsibility over the selection, acquisition, control and management of all National Reserves' is emphasized, and it is also laid down that 'the technical complexity of the problem of control and management, as well as that of selection, makes it imperative that the executive authority should be composed of persons having expert knowledge of plants and animals and their natural communities, but they should have the assistance of such administrative officers as may prove necessary. Such a body, though having executive powers in relation to National Reserves, should be available to act in an advisory capacity to the National Parks Authority as well as to those concerned with the control and management of Local Reserves, Scheduled Areas and lands owned by public bodies, and arrangements should be made for the maintenance of a close liaison between the various authorities concerned' (par. 33). With the general purport of these recommendations your Committee is in full agreement.

The N.R.I.C. further recommend that the actual administration of the National Reserves should be carried out by dividing the country 'into a suitable number of Conservancies, each under a Conservator who would have under him an adequate staff of Wardens. The Conservators would be responsible to one or more Senior Conservators, who would be charged with general supervision, and would be the link between the local officers and the National Reserves Authority. Appointments to the posts of Conservators and Senior Conservators would require careful selection, as these officers would need to combine the specialized knowledge of competent field naturalists with practical ability in the management of land' (par. 37).

Some such machinery as that proposed would certainly be necessary, but it should, in the opinion of your Committee, form part of a wider scheme for a Wild Life Service such as is suggested on pp. 30–32 of this Report.

(*b*) *Local Reserves*

'Since the primary function of this type of reserve is the preservation of sites of local, scientific, amenity and educational value, their selection, acquisition, control and management should be a matter for voluntary effort by individuals, societies and other bodies that have these interests at heart. In this field local authorities, and more particularly County Councils, have a large sphere of interest. County Councils and County Borough Councils are directly concerned in the educational and indeed in the general amenity value of nature reserves.

'The Committee therefore recommend that the powers of local authorities should be enlarged so as to enable them to purchase or contribute towards the cost of the purchase of, and to maintain, or contribute towards the cost of maintenance of, nature reserves within or without their respective areas, and whether or not such reserves are intended to be vested in them. Planning authorities also should be enabled to secure the preservation of such reserves under their Planning Schemes' (par. 40).

'The holding authority for Local Reserves may reasonably vary with the individual circumstances of acquisition. Where the purchase money and cost of upkeep are met by voluntary effort or by the County Council it may be desired to vest the reserve in the Society for the Promotion of Nature Reserves, in County Councils, or in similar bodies' (par. 42). 'Certain Local Reserves may well remain in private ownership and even under private management, but in this event some agreement should be come to between the landowner and the local body directly concerned with the continued preservation of the site. When a landowner is able and willing to bind himself and his successors in title to maintain an area selected as a Local Reserve, the agreement should if possible be made effective and binding by provisions inserted in the relevant Planning Scheme or by deed of covenant between the parties directly concerned.... It would be most desirable to secure that all reserves remaining under private management should be open to qualified scientific inspection at reasonable periods and that the owner should undertake to allow that degree of public access which would be compatible with the proper maintenance of the reserve' (par. 43).

'In the selection of the reserves and in the delimitation of their boundaries great care would have to be exercised either to include a sufficiently wide belt of land round the actual site to be protected or to secure such control over the uses of this belt as would safeguard the site from many deleterious marginal effects. The advice of the central

National Reserves Authority should invariably be sought on all questions of selection and delimitation of Local Reserves' (par. 44).

'A number of existing nature reserves are controlled and managed by local committees. This method is probably that most suitable for the Local Reserves here contemplated. The nature and the constitution of these committees would depend upon the manner in which the reserve was held, but in any event it would be desirable to secure that the County Council in whose area the reserve was situate should be represented upon them. Other obvious persons would be representatives of local, and even perhaps national, societies, and naturalists with knowledge of local conditions. The appointment and duties of conservators or wardens would be a matter for consideration by the committee of management. These committees might well control a group of Local Reserves, and where educational reserves were included, representatives of the institutions likely to make use of them should be appointed for service on these committees.

'Care should be taken to ensure that adequate scientific advice is available and is followed. The obvious body to supply such advice would be the National Reserves Authority, and their Conservators in the area should be responsible for maintaining the closest touch with these managing bodies' (par. 45).

'Local authorities should be empowered not only to acquire and hold reserves but also to make and enforce suitable bye-laws for the prevention of nuisance and damage and for the preservation of order. It is further recommended that Nature Reserves shall be included in matters to be dealt with in Planning Schemes' (par. 46).

Your Committee is in general agreement with the proposals in regard to Local Reserves contained in the foregoing paragraphs quoted from the N.R.I.C. Report, but would add the following considerations.

As we have already argued (p. 23) there is not only no valid reason why the majority of reserves should not be used for all three of the purposes for which reserves may be made, but there are great positive advantages in so using them. For this reason it is desirable that the local committees of management should usually include representatives of all three interests, i.e. members of public bodies, teachers, and naturalists, including ecologists. By their association on the committees these different types of member would learn to understand one another's interests and the ways in which each interest could be helpful to the others. Among teachers, members of the biological staffs of local universities or university colleges should certainly be included wherever possible, for they would combine the scientific and the educational interests.

It is true that there is often a single dominant motive in the proposal to make any particular reserve, which may be either intended primarily for public enjoyment or for the preservation of a particular type of wild life. In most cases these different uses need not conflict and may, on the contrary, be made to serve one another. But there are of course reserves where the effective preservation of wild life does preclude unlimited public access, and there are others suitable for public enjoyment but containing little of ecological interest. Furthermore, there are some Species Reserves where secrecy is necessary in order to prevent the depredations of unscrupulous collectors. The existence of this small minority of exceptional cases should not hinder recognition of the possibility and desirability of using most reserves for more than one purpose, even though it was originally proposed with a single end in view.

In the opinion of your Committee it is desirable that the National Reserves Authority or other central Government authority charged with the conservation of wild life (see pp. 75–76) should keep a record with full particulars of all reserves, local as well as national, which included among their objects the preservation of any kind of wild life. The Local Reserves, as is pointed out in the N.R.I.C. Report, will supplement the National Reserves in an important way, and the whole should form a system of reservation illustrating the nature and distribution of native plant and animal life. Particulars of the whole system should be published in a suitable form so as to be available to naturalists and the interested public.

6. THE NEED FOR AN EDUCATIONAL CAMPAIGN

Appreciation of the character and beauty of unspoiled country is widespread, but it is far from being universal. Interest in natural history, outside the ranks of professional naturalists, is also widely diffused, though it is perhaps true that its hold has diminished in some parts of the population during the past half-century.[1] There is probably a smaller proportion of country parsons who are naturalists to-day than at the end of last century, and the same seems to be true of working men in the north of England. Many local natural history societies are seriously weakened and others have disappeared. The causes are probably the multiplication of other interests and the greatly increased pace of modern life.

Nevertheless, it seems to your Committee that there is now a greater potential field for the development of both these interests than ever before. Owing to the development of motor traffic large numbers of town dwellers are able to visit the country more frequently and to range much farther. The need of change and refreshment that can be had in this way is more keenly felt just because of the strain of modern town life, while appreciation of natural beauty and interest in natural scenery and wild life can greatly intensify the pleasures and benefits of country excursions and sojourns.

A more widespread knowledge and understanding of the different natural types of country, their physical features and their characteristic vegetation are just what is required to build up a discriminating appreciation of rural beauty and enthusiasm for its preservation. This of course includes the farmlands which occupy most of our lowlands as well as the areas which still bear natural or semi-natural vegetation. If means can be devised of effectively spreading this sort of knowledge, the repercussions should contribute in an important way to the success of schemes for nature conservation. If sufficient people are fond enough of unspoiled country and would hate to see it disappear, their voices will gain an effective hearing.

There are several ways in which such knowledge could be disseminated, and the following may be suggested.

(1) The preparation of a series of attractive illustrated regional booklets dealing in the first place with favourite routes for trips by motor coach and private car from centres of population, later with more remote areas. Each booklet should deal with the physical features, geology, soils, natural vegetation and agricultural use of the area, together with the towns and villages, all of course in strictly untechnical language. Attention should be specially drawn to beautiful and characteristic features of all kinds. Brief historical

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[1] An exception is the recent vigorous growth of interest in our native birds, of which the great increase of bird watching and bird photography and the immense success of the Royal Society for the Protection of Birds are strong evidence.

remarks should be introduced and current or probable future trends of development noted. The characteristics of 'beauty spots', which are often the goals of motor trips, should be fully described, and the opportunity taken to introduce anti-litter propaganda and to discourage the defacement of nature, for instance by wholesale and indiscriminate plucking of flowers and branches and the uprooting of plants. Any existing Nature Reserves in the region, and their purposes, should be mentioned, except in the case of those Species Reserves in regard to which it is desirable to maintain secrecy.

If such booklets were skilfully written from full knowledge, in a simple attractive style, avoiding technicalities and also all tendency to 'write down' to the reader, they should have a very good sale and a gradual but powerful educational influence. Much can be said for making them official publications, as are the bulletins and circulars of the 'Fish and Wild Life Service' of the U.S. Department of the Interior; but alternatively the scheme should be attractive to publishers.

(2) Nature Reserves, both National and Local, except those which are unsuitable for the purpose, should be made centres of education in field natural history. A large part of the public support that can be gained for nature conservation must arise from the stimulation of local interest in local country and its vegetation and animal life. Demonstrations of the nature and character of unspoiled samples such as are set apart as nature reserves will be the best means of arousing interest. To these should be added explanations and demonstrations of the effects of various kinds of human activity on similar country which can be seen in the same neighbourhood. Interest should be primarily directed to types of natural and semi-natural vegetation, the plants of which they are composed, and the changes they undergo, both when let alone and when subjected to various treatments, e.g. the pasturing of grassland, the burning of heaths, etc.: for it is upon the vegetation and its changes that the character of British scenery mainly depends.

In this educational function of reserves local schools could take a great part. Members of the biological staffs of local universities, where such institutions exist in the neighbourhood, would certainly be willing to help, and so would local natural history societies.

(3) Descriptions of the different reserves should be prepared in pamphlet form and should be available for sale at the reserve. They should be more detailed and thorough than the booklets proposed under (1), but at the same time easily understood by non-specialists, though with more than a purely popular appeal. These pamphlets would serve as handbooks to the reserves for all who used them, including the schools. Those relating to the National Reserves would be official publications.

(4) Lectures and field trips should be organized in connexion with the reserves by competent naturalists, whether members of university staffs, schoolmasters, members of local natural history societies or others.

7. The establishment of a National Wild-Life Service

The concluding words of the N.R.I.C. Report (par. 52 and Summary, par. xlv) are these: 'The Government should take formal responsibility for the conservation of native wild life, both plant and animal.'

Your Committee heartily welcomes this declaration which they believe to be the key to the success of any comprehensive scheme of conservation. What is wanted is first of all unequivocal public recognition of nature conservation as a national interest, implemented by a national scheme and supplemented by local effort.

The establishment of a series of National Nature Reserves is an indispensable and invaluable step, but alone it is not enough. As we have seen, Nature Reserves are not by themselves sufficient to conserve our native birds and mammals. What is required is continuous study of the distribution, density and habits of each species and of the interrelationships between them, not only those of predator and prey but many others. Such study is both a scientific and an economic interest, as is shown by the very successful work of the Bureau of Animal Population at Oxford, particularly with the small rodents. The 'control' of pests, it has been well said, is the mirror image of conservation. Exactly the same type of knowledge is required for one as for the other. Control in the proper sense, i.e. regulation, is what must be aimed at, and scientifically acquired knowledge is its essential prerequisite. In order to gain and apply such knowledge on a sufficiently comprehensive scale a national service is necessary.

But it is not only the problems of birds and mammals which are involved. Invertebrate animals and plants present a host of problems, all of great scientific interest, and many of economic importance as well. A National Wild Life Service which would be an effective organ of nature conservation should embrace the whole field of the native flora and fauna, and only in this way we believe can a really successful scheme of nature conservation be established. We have an example in the American 'Fish and Wild Life Service' of the Department of the Interior, though this does not include plants and invertebrates. There would be great advantage in making the British scheme comprehensive of all wild life because the whole forms a great web with the most complex interrelations between its different strands, and increased knowledge of parts of this web is continually throwing light on other parts.

In such a service the National Nature Reserves would play an important part, for they would be natural centres of observation and experiment. Experimental use would in no way interfere with conservational and educational functions. Only small portions would be used for experiments calculated to change the vegetation or animal population, so that the aesthetic aspects of the whole reserve would not be affected. And the carrying on of experiments in a reserve would actually enhance their educational value. The same sort of work could be carried on in Local Reserves, but subject of course to the approval of the local committees of management.

Part of the work of a Wild Life Service would be the supervision of the National Nature Reserves, the function of the Conservators under the N.R.I.C. scheme. Conservators and Wardens of National Reserves would indeed be officers of the Service. But continuous research on the problems of conservation and control, whether within or outside the reserves, would be an essential part of the duties of the Service, and these problems, as we have seen, are always, at bottom, ecological problems. A considerable degree of specialization would be necessary, for the habits and density of a population of mammals or birds, for example, is a very different subject from the control of the plant population of a reserve. But a thorough general acquaintance with natural history in the field would be the proper foundation of the training of all officers, who should always be alive to possible interrelations, which are often unsuspected and subtle, between organisms of widely different types.

It is suggested that it would be preferable to constitute the central authority of a Wild Life Service as a separate body under the Privy Council, with a status similar to that of the Medical Research Council, and to make the selection and supervision of National Nature Reserves part of its work, rather than to set up a National Reserves

Authority parallel with the National Parks Authority and to place it under the Ministry of Town and Country Planning, as the N.R.I.C. Report proposes, or under any other existing Ministry. It would be well to keep the Service independent of the policy of a Ministry with different primary purposes and to enable it to create its own policy and traditions.

SUMMARY

1. Despite the immense change in the face of the country from its original condition there remain considerable tracts covered by wild vegetation with the multitudes of lower animals it harbours. Though the larger carnivorous mammals have disappeared and the larger predatory birds are greatly reduced, many smaller mammals and a great bird population still exist. The whole of this wild life is part of the national heritage, valuable to the nation in many different ways, and it is threatened with serious and widespread destruction in the immediate future. The means of preserving as much as is compatible with other objects of paramount national importance require careful consideration. The only method of preserving wild vegetation with its population of lower animals is to set aside areas as nature reserves. The higher animals and birds require separate treatment.

2. The first object of nature preservation, which has the widest support, is maintenance of the beauty and interest of characteristic British scenery. In the past this was largely preserved by the existence of large private estates which are probably destined to disappear. Public action is the only alternative means of preventing destructive change. In future 'country planning' rival claims to the use of land, both between different possible economic uses and between these and the preservation of natural scenery, will have to be decided, and give-and-take will be necessary. The scientific claim to the preservation of wild life depends very largely on the modern science of ecology which has important economic as well as purely scientific value, and the ecological interest coincides very largely with the aesthetic and sentimental, because both demand the preservation of considerable tracts of unspoiled vegetation with its accompanying animal life. Education in natural history is not only important in itself, but it enhances appreciation of the natural beauty of landscape, and good education of this sort depends on the advance of ecology. Thus each of these three interests reinforces the others.

3. The problems of nature conservation must be viewed against the human background. The increase of motor transport and the great effectiveness of modern means of destruction press hardly on all kinds of wild life. Such means are largely used to further sectional interests and are constantly 'upsetting the balance of nature'. Just what should be destroyed and what preserved should be a matter of public policy, and the balance aimed at should be the ecological expression of the resultants of the different human desires. The increased attention to forestry with its inevitable replacement of much natural and semi-natural woodland (too often derelict) by economically managed forests and plantations of conifers is discussed at some length as an example of the pursuit, under national authority, of an economic interest which has wide repercussions on nature conservation. It is suggested that a wider policy would enable the Commission to play an important part in the conservation of nature as well as to develop great new forests, provided the whole land surface were available for inclusion in a comprehensive scheme. Game preservation has two opposite effects on wild life. It preserves much natural vegetation (such as deciduous woods and copses for pheasants, heath, moor and mountain for grouse and red deer), with

the animals which inhabit it, so far as these are not inimical to the game itself: on the other hand, predators are ruthlessly destroyed, and this has led to great increases in the numbers of small rodents, which do serious damage to crops and young trees. If all game preserving were to cease and no alternative protection put in its place, we should soon lose most of our existing wild-life habitats, at least below an altitude of 1000 or 1500 ft.

Love of nature has probably become more widespread in recent years (though natural history as such has been losing its hold on parts of the population), and a notable instance is the attachment to wild birds. Such sentiments cannot be ignored in country planning but must be considered along with economic interests.

4. (i) The establishment of National Parks and 'Scheduled Areas', though they would safeguard much natural vegetation, cannot meet the whole of the scientific needs. Many smaller areas (Nature Reserves) under management primarily designed to meet these needs are required. It is proposed by the semi-official Nature Reserves Investigation Committee that *National Nature Reserves*, to be acquired by the State and administered by a State authority, representing all the important British types of natural habitat and natural plant community, should be distinguished from *Local Nature Reserves* acquired or held locally under various arrangements with their present owners and used for scientific, educational or 'amenity' purposes. Informed and careful scientific management is necessary for nearly all reserves. Most areas which would be reserved depend for part of their character on human activity in the past and present, and it is necessary that this activity should be continued or replaced by other means if their character, on which the whole value of the areas depend, is to be retained. Areas which have always been immune or nearly immune from human interference are few, but naturally of great ecological importance. In general they require less active management than the semi-natural areas. But the great majority of reserves require expert management. Though the primary functions of National Parks are different, and their administration will properly be entrusted to a separate authority, yet the maintenance of their natural vegetation must always be a primary object if their beauty is to be preserved, and to achieve this expert advice will constantly be necessary. Much of the knowledge required has been gained through the ecological work of recent years, and this will be constantly added to as fresh research is undertaken. National and Local Nature Reserves will afford exceptionally good opportunities for such research.

(ii) Invertebrate animals such as molluscs, insects and other groups are automatically protected if the vegetation they inhabit remains undisturbed. Particular tracts of vegetation known to harbour rare species should be reserved and the activities of collectors restricted.

(iii) The further diminution of fresh-water pollution is the most important measure that can be taken for the conservation of fish populations, and this is already strongly supported by the powerful angling interests. Reservation of particular ponds and small lakes for the sake of their plant life, water birds, etc., may no doubt reduce or destroy the water as a habitat for fish, but the number of reserves required for such purposes is quite limited, and in some cases appropriate management could provide for both interests.

(iv) Most of the twelve native species of amphibia and reptiles are of widespread distribution and in no serious danger, but three species are very local and the areas in which they occur contain in fact very suitable sites for nature reserves (probably National) on several different grounds.

(v) Birds and mammals, both because of their great powers of movement and because certain species directly involve human interests, cannot be conserved simply by reserving particular areas. The problem of conservation involves that of control and always becomes one of attaining and preserving a certain optimum density and distribution of individual species in different parts of the country. This necessitates the application of the results of research to the field problem. (*a*) Proper balancing of various material and cultural claims is a necessary preliminary to a decision on the precise goals of control (in the sense of 'regulation'). Adequate publicity and increase of public knowledge and interest are necessary to obtain popular support for the measures taken. Sectional interests give rise to very different attitudes to different species of animal. Shooting men wish to increase the populations of certain native and introduced game birds and to see those birds and mammals which prey upon them diminished or wiped out. This desire has led to a great scarcity of predators. The fox stands in an exceptional position because it is both a predator and itself an object of sport. The introduced rabbit throughout its long history in this country illustrates the fluctuations and conflicts of human interests. There is a case for allowing the continued existence of moderate and controlled rabbit populations in some areas. There is also a case for maintaining a moderate (rather low) population of the common vole in hill regions, though in excessive numbers it does serious damage to young plantations. The two squirrels (red and grey), endemic races of Hebridean mice, seals on the Cornish coast, and the proposed abolition of hedgerows and small copses in agricultural country provide examples, among many others, of conflicts between real or supposed interests which can only be resolved by control based on a just balancing of the reality and importance of the different interests. (*b*) Many different animals have been introduced into this country at various times and with various objects. Some of them have done a lot of harm, unconsidered by the introducers. (*c*) The main uses of reserves for vertebrate animals are to protect localized breeding stocks, roosting aggregations of bats, and very local species which have no great powers of movement. Many birds and the larger mammals, which have such powers, cannot be safeguarded in reserves. General control is required and this must be based on accurate knowledge of the habits of the different species, knowledge which can only be obtained by research.

(vi) All naturalists have an interest in prevention of the extinction of rare species. 'Sanctuaries' or—better—'Species Reserves' for this purpose must, however, be examples of the particular community in which the species naturally occurs, and while the occurrence of the particular species adds to its interest the choice of sample communities for preservation cannot be limited on that ground.

5. Haphazard procedure in nature reservation, valuable as it has been in the past, now requires to be replaced by a systematic and comprehensive plan of national scope.

(i) The N.R.I.C. propose that a series of *National Nature Reserves* should be made, selected and managed so as to ensure the survival of all the main natural and semi-natural communities of plants and animals for the purpose of serious study. The location of these must depend on the natural distribution of the communities in question, their management must be expert and subjected to unified direction with full responsibility at the centre. This proposal has the complete support of your Committee.

(ii) The type of reserve described in (i) is called by the N.R.I.C. a 'Habitat Reserve'. Besides this they propose the establishment of 'Species Reserves', some of which would be National Reserves and which are intended to secure the survival of rare or very local species. Since it is admitted that a Species Reserves would really be a Habitat Reserve which contained one or more rare species, and would require exactly the same kind of management, it would seem unnecessary to draw a sharp distinction between the two. It would seem sufficient to select certain Habitat Reserves not only because they contained good examples of natural communities but also because they contained rare species—a course all naturalists would desire. A reserve made on these grounds should always be much larger than the area occupied by the rare species, to allow room for possible expansion of occupied area, or shift of the species. It is always the habitat, as the essential condition of the continued existence of the species, which it is important to safeguard.

(iii) The 'Amenity' and 'Educational' Reserves contemplated by the N.R.I.C. since they 'subserve local rather than national needs' are placed under the category of *Local Nature Reserves*. Your Committee wishes to stress the point that most, though not quite all, nature reserves, national as well as local, can fulfil all three functions of a reserve—scientific, educational, and 'amenity'—without damage to any, and that it is most desirable that all which can should be made to do so, because in this way they will serve the widest range of interest and obtain the greatest measure of public support. The general conclusion seems to be that all nature reserves must really be 'habitat reserves', and that the maintenance of their threefold value depends essentially on ecologically instructed management, which is alone competent to decide what can be permitted and what disallowed in the conditions of particular reserves.

(iv) Scattered through the country there is already a considerable number of reserves which have been made for diverse purposes, and many of them are vested in the National Trust. Most of these have been made with the object of securing to the public the use and enjoyment of areas of natural beauty, but in some of them conditions permit of scientific work within the reserve. A few belong to the Society for the Promotion of Nature Reserves, and these are selected because they are of interest to naturalists. Besides these there are others belonging to local societies, trusts or private individuals. Such reservations will no doubt continue to be made whether a national scheme is adopted or not, and since they will usually be made mainly by local effort their ownership and administration must naturally be determined by local wishes. As in the case of National Reserves, it seems unnecessary to divide Local Reserves into rigid categories, since many of them can be so well employed for more than one purpose, and where possible it is highly desirable that the different functions should be carried on side by side. An exception must be made in the case of those reserves intended to promote the interests of naturalists and in fact unsuitable for the enjoyment of public amenities. But usually the various interests can be harmonized by enlightened management, sometimes by setting aside part of the reserve for scientific work and allowing the public free access to the rest.

(v) The proposal by the N.R.I.C. to schedule certain areas in which further development would be prohibited or drastically restricted, without interfering in any way with the present use of the land or the existing free movement of the public, is warmly welcomed by your Committee. If an adequate number of well-selected areas are thus scheduled, a large part of our national heritage of beauty will be maintained, both that which depends on natural landscape and that which owes its character to rural settlement and agriculture. Incidentally, as it were, many sites of great interest and importance to the ecologist will be preserved, apart from the formation of specific nature reserves. It is suggested that in southern and eastern England there are five main types of country of which large areas should be scheduled: (1) parts of the coastline that are still unspoiled, with their sand dunes, salt marshes and cliffs, (2) the chalk country with its downland and beechwood, (3) heathland, (4) clayland bearing coppices with oak standards and grassland, and (5) the river valleys of East Norfolk with their rivers, broads and still unspoiled fenland.

(vi) (*a*) The N.R.I.C. recommends the establishment of a central National Reserves Authority having full executive responsibility over the control and management of all National Nature Reserves and composed of persons having expert knowledge of plants and animals and their natural communities. It should be available to act in an advisory capacity to the National Parks Authority as well as to those concerned with the control and management of Local Reserves, Scheduled Areas, and lands owned by public bodies. With these recommendations your Committee is in general agreement. The N.R.I.C. further recommends that the National Reserves should be administered by Conservators (with Wardens under them), and one or more Senior Conservators who would be the link between the Conservators and the National Reserves Authority. The qualifications of the Conservators and Senior Conservators would have to combine the specialized knowledge of competent field naturalists with practical ability in the management of land. Some such machinery as that proposed would certainly be necessary, but your Committee is of opinion that it should form part of a wider scheme of the nature of a 'Wild Life Service' (see Section 7).

(*b*) The N.R.I.C. makes a number of detailed recommendations about the selection and classification of Local Nature Reserves, their tenure, management by local committees, the representation of various interests on these committees, and the necessity of advice from the National Reserves Authority. With these your Committee is in general agreement, but would suggest that since many nature reserves can and should be used for all three purposes—scientific, educational and public enjoyment—it is desirable that the local committees of all such reserves should include representatives of the three interests, who would by their association on the committee learn to understand one another's interests and the ways in which each interest could be helpful to the others. Wherever possible members of the biological staffs of local Universities and University Colleges should be included, as these would combine scientific and educational interests. Your Committee is of opinion that the National Reserves Authority or other central authority charged with the conservation of wild life should keep records with full particulars of all reserves, local as well as national, which included among their objects the preservation of any kind of wild life, and should make them available to naturalists and the interested public by appropriate publications.

6. It seems to your Committee that there is now a greater potential field for the development of appreciation of the character and beauty of unspoiled country and of interest in natural history than ever before. A more widespread knowledge and understanding of the different natural types of country, of their physical features and their vegetation, is just what is required to build up a discriminating appreciation of rural beauty and enthusiasm for its preservation, and an educational campaign is necessary. The repercussions should contribute in an important degree to the success of schemes for nature conservation. Such an educational campaign could be promoted in several ways, e.g. by the preparation of a series of attractive popular illustrated booklets dealing with the physical features, geology, soils, natural vegetation and agricultural uses of the country on popular motor routes from centres of population; by making suitable Nature

Reserves, both National and Local, centres of education in field natural history, thus stimulating local interest in local country and its vegetation and animal life; by publishing untechnical but thorough descriptions of the different reserves in pamphlet form to be purchasable at the reserve; by organizing lectures and field trips conducted by competent naturalists in connexion with the different reserves.

7. 'The Government should take formal responsibility for the conservation of native wild life, both plant and animal.' These concluding words of the N.R.I.C. Report are warmly welcomed by your Committee, which believes that they contain the key to the success of any comprehensive scheme of conservation. In such a scheme the establishment of a series of National Nature Reserves is an indispensable and invaluable step, but by itself it is not enough. Nature Reserves are not sufficient to conserve our native birds and mammals. What is wanted is continuous study of the distribution, density and habits of each species and of the relationships between them. Such study is both a scientific and an economic interest. What can be done in this field is shown by the work of the Bureau of Animal Population, especially on small rodents, and of the Edward Grey Institute of Ornithology at Oxford. Control of pests is the mirror image of conservation. Exactly the same kind of knowledge is required for one as for the other. In order to gain such knowledge on a sufficiently comprehensive scale a national service is required. It is not only the problems of birds and mammals which are involved. Invertebrate animals and plants present a host of problems, all of great scientific interest and many of economic importance as well. We need only refer to insect and fungal pests and their host plants and animals. There is a great deal to be said for establishing a National Wild Life Service to embrace the whole flora and fauna, and such a service we believe is necessary if we are to have a really effective organ of nature conservation. In such a service the National Nature Reserves would play an important part, for they would be natural centres of observation and experiment, and these need in no way interfere with their conservational functions, since experiments calculated to change their aspect would be restricted to small parts of the reserve. The educational function would actually gain by such work. Conservators and Wardens of the National Reserves would be officers of the proposed Service. But whether they themselves could undertake it or not, continuous scientific research on the problems underlying practical conservation and control would be an essential function of the Service.

It is suggested that it might be preferable to constitute the central authority of a Wild Life Service as an independent body under the Privy Council, with a status similar to that of the Medical Research Council, rather than assign it to the Ministry of Town and Country Planning or any other existing Ministry.

GENERAL CONCLUSIONS

Your Committee considers that the *Report of the Nature Reserves Investigation Committee* is a very valuable document. With most of the considerations and recommendations of that Report they are in close agreement.

They particularly welcome the claim that 'the Government should take formal responsibility for the conservation of native wild life, both plant and animal', and the recommendation that a number of National Nature Reserves, representing all the important types of British vegetation with accompanying animals, should be acquired by the State and placed under a central State Authority with expert personnel; while the continued acquirement locally of Local Nature Reserves to supplement the National Reserves should be encouraged and advice from the Central Authority on their management should be freely available. They also welcome the suggestion to 'schedule' typical areas in which destructive 'development' would be prohibited.

Your Committee would, however, suggest that the division of Reserves proposed by the N.R.I.C. into Habitat, Species, Amenity, and Educational Reserves should not be sharply defined and rigorously carried out. In the majority of Reserves, both national and local, the functions of maintaining the wild life for scientific study, of using it for educational purposes, and for the enjoyment of its 'amenities' can be carried on side by side with great reciprocal advantages, each interest helping the others. The essential condition, however, is the careful regulation of these various activities by expert management. There are also certain reserves in which one of them would have to be made paramount, with limitation or possible exclusion, temporary or permanent, of the others.

Further, your Committee would point out that some of our animal wild life, more particularly birds and mammals, cannot be conserved by means of reserves alone, but requires careful regulation of the densities of the populations of the different species, for which continuous research into their habits and distribution is essential. For this reason, and in order to promote and increase ecological knowledge, which is important in the national interest, both scientifically and economically, your Committee recommend the establishment of a National Wild Life Service, embracing both plants and animals, whose functions would include continuous research as well as the administration of National Nature Reserves; and they suggest that its governing body should be given an independent position under the Privy Council. Only in this way, it is believed, can Government adequately discharge the responsibility for the conservation of wild life which they are now invited to assume.

BRITISH ECOLOGICAL SOCIETY

ECOLOGICAL PRINCIPLES INVOLVED IN THE PRACTICE OF FORESTRY

Joint meeting between the Society and the forestry societies of Great Britain—Society of Foresters of Great Britain, Royal Scottish Forestry Society, Royal English Forestry Society, Empire Forestry Association.

The proceedings were opened at 10.30 a.m. on 2 July 1943, in the rooms of the Linnaean Society, Burlington House, Piccadilly, London.

Captain C. Diver, in the Chair, expressed the regret of the Society that the President, Dr H. Godwin, was unable, because of illness, to preside. He referred to the growing necessity for liaison between foresters and ecologists, which the present meeting was designed to further. Welcoming the Forestry Commission's readiness to establish Ecological Reserves, he expressed the hope that this policy would be maintained, and given wider expression yet, at an early date.

Professor A. G. Tansley, F.R.S. First of all I must warmly welcome the desire of the Forestry Commission, as recently expressed by its Chairman, to make closer contact with ecology. And on behalf of the British Ecological Society, whose President, as we must all regret, is unfortunately prevented by illness from taking the chair to-day, I am sure I can reciprocate that desire. For not only can foresters find in ecological work much that will help them to a scientific rationale of their practical operations; ecologists can find in the results of those operations, whether successful or unsuccessful, invaluable material for learning more about the reactions of growing trees to different conditions. Every plantation is an ecological experiment, and on a scale which working ecologists rarely have the opportunity to employ.

Scientific ecology, we must remember, is a very young subject of research, almost entirely a product of the present century, and only developed energetically since the last war. It has had many difficulties to face, though to-day, I am glad to say, its influence is rapidly extending. Not the least of its difficulties has been the lack of sufficiently extensive opportunities for adequate ecological experiments, without which the science cannot progress. I know very little of practical forestry, and I have often wished when I was teaching forestry students their elementary botany and always from the general point of view of ecology, that I had had a practical training both in forestry and agriculture, just as I wished I had had a practical training in medicine when I was teaching biology to medical students. For just as scientific medicine is really a branch of applied biology, so forestry and agriculture may be regarded as branches of applied ecology. But the practical arts of medicine and agriculture are much older than the corresponding branches of pure science—agriculture some thousands of years, forestry in Britain two or three centuries, while ecology is a growth, so to speak, of yesterday. Consequently a great deal of largely empirical knowledge has been accumulated, while ecology is only now beginning to be in a position to attempt explanations of some of the facts observed. What we need above everything to increase our knowledge of the ecology of woodlands, is, as I have already insisted, continuous opportunity for access to and study of planting experiments, together with the power of suggesting different variations and forms of control which seem likely to lead to increased insight into the factors at work. This line of thought clearly envisages a very close collaboration between foresters and ecologists.

The Forestry Commission has itself conducted many planting experiments and studies of tree growth intended to throw light on the practical difficulties it has encountered. In a broad sense such work is ecological work, but it is, of course, designed, and must be designed, to solve specific practical problems rather than to arrive at new scientific generalizations that can be used to guide future developments. Exactly the same distinction exists in industry, where technological research is necessary for the solution of specific industrial problems, while pure research in the basic sciences, conducted with the aim of increasing scientific knowledge, forms the foundation for new general advances. That is not to say that practical problems cannot provide starting points for pure research. On the contrary they can, and constantly do. Rayner's work on mycorrhiza and Neilson Jones's on the toxicity of Bagshot Sand soils at Wareham, where pine obstinately failed to make good growth, are examples of research which used practical difficulties as starting-points, though Rayner's contributions to our knowledge of mycorrhiza were begun at a much earlier date. The point is that research in pure science must be free to be pursued wherever it may lead. It may or may not immediately throw direct light on current practical problems. When it does, the whole subject is more brightly and widely illuminated because the research is not narrowly tied to a particular problem. Both kinds of research are necessary, and it is only by the combination of the two that the most fruitful progress is made.

Sir Roy Robinson has put forward two working hypotheses which he calls the hypothesis of *accelerated succession* and the hypothesis of the *silvicultural stream*. Both are based on the general theory of the succession of vegetation which is one of the cardinal theories of plant ecology.

The hypothesis of accelerated succession states that 'in the natural afforestation of difficult sites some species are pioneers and some are successors. It is not feasible by artificial means to bring in the successors in advance of the pioneers. It is possible, however, to accelerate the natural succession by mixed planting of pioneers and successors, and by appropriate thinning treatment to complete the succession in the course of a single rotation. A successor on one site may be a pioneer on another.'

It is not only on 'difficult sites' that there is a regular succession of vegetation in 'natural afforestation' and a typical sequence of pioneers and successors among the species colonizing the site. That is a universal phenomenon following constant general laws, though the details are exceedingly various according to the nature of the climate and soil and the species available for colonization. The complete sequence begins with a bare site unoccupied by vegetation, and trees rarely figure among the pioneer plants, though they may sometimes do so as on wet alluvium newly laid down by a river. But the vast majority of bare sites are, to begin with, difficult or impossible for trees, which cannot succeed until a soil has been created on a bare rock surface, or a raw soil mixed with the humus left by the pioneer plants. Even when trees do appear some species come before others because they can tolerate relatively unfavourable conditions and also often because their parents produced abundance of seed easily transported to the site in large quantities. These pioneer trees, of which birch and pine are good examples in this country, ultimately give way to heavy-seeded, more exacting and shade-bearing trees, usually of slower growth, such as beech and spruce, which eventually overshadow, and kill out the light-demanding pioneers. Among the successors some become dominant and form the so-called 'climax forest' natural to the region. But because they are more exacting in their demands upon the soil they only succeed on soils which are capable of meeting those demands. Thus among the natural spruce forests of central Sweden there are areas of shallow soil, overlying flattish rock surfaces, which are occupied by pine, with no spruce, because the soil has not developed to meet the demands of spruce. Pine (with birch) is a natural pioneer, preceding spruce in these forests, but when spruce, the climax dominant, comes in and can flourish, pine is naturally eliminated. On the areas referred to pine takes the place of the climax dominant and forms what ecologists call a 'subclimax'. As Sir Roy Robinson points out, we are still largely ignorant of the exact factors which prepare the way for successors or climax dominants, though we know something about them in a general way. Almost certainly they differ in detail in different cases, but as he shows, there is good evidence that the earlier colonists often promote, directly or indirectly, the success of the later ones. Hence the practice of mixed planting which artificially brings these beneficial effects into operation.

The 'good' sites for planting are those in which the soil is well developed, well provided with available nutrient salts, well aerated, and retaining a sufficient supply of the right kind of humus, as on good old pasture grassland or good arable land. Here we have conditions corresponding with a *late* stage of succession, and exacting trees can be planted at once. The 'difficult' sites are those in which previous treatment of the land has reduced it to conditions corresponding with an *early* stage of natural succession, in which some or all of the favourable factors mentioned above are absent and climax trees will not succeed without preparation. The two types of difficult sites chosen by Sir Roy as examples are, first, those comparatively well-drained soils of the old acidic rocks and some of the more recent sands on which heather quickly develops as the result of enclosure and cessation of grazing or burning, and secondly the shallow chalk soils of the south and east of England. On the first type the soil is typically poor in nutrient salts and on the second it is shallow and dry, with insufficient humus.

The procedure suggested by Sir Roy—'mixed planting of pioneers and successors'—brings about a condition comparable with that obtaining in what is sometimes called 'telescoped succession', i.e. natural succession in which two or more species of tree, including pioneers and successors, sow themselves on a site at about the same time. The quicker growing pioneers, which are better suited by the soil in its undeveloped state, become dominant first, though both start at the same time, and later the slower growing successors, favoured by the shelter of the pioneers and/or by changes brought about in the soil by the vegetation cover, grow up among the pioneers and eventually suppress them and become dominant. Alone they could not have done so. It is clear that mixed planting of pioneers and successors in suitable, empirically determined proportions, imitates this natural process, and should result in a successful crop of the successor tree which is desired.

Sir Roy's first example is Scots pine and Douglas fir in Swaffham Forest. A similar example he gives is in the New Forest, where Douglas, common ('Norway') spruce and Sitka spruce did not succeed on heather areas until Scots pine had reseeded the ground from adjacent trees. Ecologists have long been very familiar with the ability of Scots pine to grow up among thick heather and eventually to convert a heather area into a pinewood. I remember, many years ago, making a count of pine seedlings among thick heather on a common on the borders of Surrey and Kent, and finding an average of one seedling to every square yard. These came from a mature pinewood about 100 yards away. Some of the seedlings were smothered by the heather, but many came through, and the common was dotted with vigorous pine seedlings and saplings of all ages. During the last war all the pine was felled, and some years later the area was covered with dense young birchwood—birch being the other pioneer tree on such soils—owing to the drastic diminution of the pine seed-parents. Oak and beech were present on the site and were actually dominant on neighbouring areas, but whether they would eventually have followed pine on this particular area could not be determined because of constant disturbance by such factors as rabbit attack, grazing and gravel digging. This perpetual interference is one of the greatest handicaps of ecologists in determining the natural course of succession in native British woodlands.

Other examples given by Sir Roy are on the old acidic rocks of the hill country of the west and north. In one of these the planting of pine not only enabled interplanted spruce to succeed but extended its favourable influence to two or three adjacent rows of pure spruce. Here we are faced with the question, in a particularly striking form, of what exactly are the ecological factors through which pine affects spruce. Ecologists have been largely occupied hitherto in describing the facts of natural succession, but we can have no thorough knowledge of a succession until we have discovered the actual effective factors which enable one kind of tree to succeed in the presence of another but not alone. In some cases, part at least of the effect seems obvious enough, but in others it is still unexplained. Only carefully designed experiments will discover the actual factors at work, and this is essentially the business of the ecologist. It is clear, I think, that successful work of this kind would be of great use to the practical forester because it would enable him to direct his planting on the secure foundation of adequate knowledge of the factors involved, and not merely by empirical results the causes of which he does not understand.

The other type of difficult site discussed by Sir Roy is chalk down. Here the natural forest trees are ash and beech, and it has been shown by Dr Watt in his exhaustive studies of natural succession in the Goodwood region and on the Chilterns that ash precedes beech on the shallow chalk soils proper, while ash and oak precede beech on the deeper loam soils of the chalk plateaux. In both cases the trees are normally preceded by a scrub phase, of juniper, hawthorn and other shrubs, the scrub providing the conditions in which the trees can succeed. The Forestry Commission has found that not only Scots, Corsican and Austrian pine, but also Norway spruce, will act as an effective 'nurse' for ash and beech on such sites. This is an unexpected example of a tree which is the dominant of climax forest in its own climatic region acting as an effective pioneer when planted in quite different conditions.

Sir Roy Robinson's second working hypothesis is that 'in the silvicultural treatment of woodlands the most effective methods are those which proceed in the direction of a natural succession of vegetation'. The concept of a 'silvicultural stream' thus postulated is an example of following intelligently the processes of nature and adapting them to human requirements. In other words we have to learn to understand nature before we can effectively control her. I entirely agree with Sir Roy's suggestion that, in undertaking silvicultural work, the point of entry into the natural scheme of succession and the direction of flow should first be determined, and that here is a field of ecological research which should prove useful to the forester. In the case of our native woodlands the phases of most successions are already pretty well known in outline as the result of ecological work during the past twenty-five years. But we have to recognize that the Forestry Commission is mainly dealing with exotic trees, and that the actual requirements of these, and consequently the places they can be made to take in an artificial silvicultural succession, are still very incompletely understood. I suggest that ecologists should make separate studies of the chief important species of exotic conifers used by the Commission, e.g. Japanese larch, Corsican and Mountain pines, Douglas fir, Sitka and Norway spruce, *Thuja plicata* and *Tsuga heterophylla,* their behaviour under different British conditions of climate and soil, and their relations to other species with which they may be planted or sown. Such studies should be entirely free, i.e. they should be directed to learning as much as possible about the life and behaviour of each species rather than to the solution of any particular practical problem. In this way facts may be demonstrated which may ultimately prove of crucial value to practical forestry but which may be overlooked if the investigations are narrowly circumscribed. But there would be every reason to choose first of all those species which are of most importance to British Forestry and in the case of which practical difficulties have arisen because of defects in our knowledge.

In regard to the 'silvicultural stream' I may repeat what I have already said, that the crucial point for research is discovery of the actual factors which enable one tree to succeed only in the presence of another species, or, to put the point more generally, of the intimate nature of the processes which lead from one phase of succession to the next. Sir Roy Robinson alludes to this when he writes of 'the way in which the pioneer prepares the way for the successor species'.

These two lines of inquiry, then, I offer as suggestions of the ways in which ecologists can give the greatest help to forestry, and I very much hope the Commission will see its way to make them possible. I expect a new development of activity in ecology after the end of the present war, comparable with, but greater than, that which occurred after the last war. To give such a development adequate scope ecologists need wider opportunities, and, of course, the means of livelihood. The ability and enthusiasm are there all right, as has been abundantly proved by the ecological work of the last twenty-five years.

One other topic I should like to refer to before I sit down. The British Ecological Society will shortly publish a Report on Nature Conservation. In this will be found some discussion of the possible role of the Forestry Commission in this important matter. It is no use disguising the fact that widespread alarm has been aroused by the great scheme of afforestation designed by the Commission for the post-war period. This is mainly because conifers greatly preponderate in the planting programme, and conifer planting on a large scale in the English lowlands will entirely alter the character of the English landscape, which depends to a very great degree, especially in the southern counties, on the presence of deciduous woodland. This alarm is shared by ecologists who are deeply interested in the continued existence of woodland composed of our native trees such as oak, beech, ash, birch and alder. Descendants of our original native forests, more or less modified and more or less replanted, still exist in many places growing on their natural characteristic soils, and they form an important part of the primary material available for ecological work. It is therefore an outstanding interest of the British Ecological Society that at least extensive samples of these woodlands should be preserved.

Two facts, essentially relevant to this question, are clearly recognized by the Society. The first is that very many of these woods are in a deplorable condition from the forestry point of view and that many also have been depleted by war-time demands. A considerable proportion have been neglected and often badly maltreated in the past owing to a variety of causes. Some at least could, however, be brought into good condition under proper management and with judicious planting here and there so that they could eventually be exploitable for timber. Those quite depleted must of course be replanted. We desire to see at least considerable parts of these deciduous woods maintained as such and not replanted with conifers. If the Commission were to see its way to work on such lines it could make a very significant contribution to the conservation of nature in the English landscape, more particularly perhaps in the south-eastern counties whose climate is essentially a climate of deciduous forest and which at present have a far larger proportion of their areas under this type of woodland than has any other part of the country. We feel that the Commission bears a great responsibility in this matter.

The other relevant fact to which I alluded is that the demand which the Forestry Commission has to meet is mainly a demand for soft wood, i.e. coniferous timber, and it is of no use for us to stop at telling them that deciduous woodland ought to be preserved when the main object must be the production of coniferous forest. At this point we suggest, as ecologists, that there are two areas in which coniferous forest is ecologically in place. One is the 'highland region' of the north and west of Great Britain, not the so-called Scottish Highlands alone, but the whole region of older rocks known to geographers as the 'highland region'. The other is the heathland of the sandy soils scattered through the English lowlands. In the highland region both climate and soil are relatively unsuited and often impossible for agriculture, and the region is now occupied mainly by moorland and hill grassland. It is, however, a prehistorical accident, so to speak, that this region has contained no native coniferous tree except the Scots pine in post-glacial times, and there is no ecological reason why we should not now supply the deficiency in response to the demand for coniferous wood. This indeed the Commission is already doing on a fairly large scale, but we suggest that a comprehensive scheme should be extended over the whole 'highland region', which would of course involve an overriding right to use the land for national purposes. The diminution of food and wool (sheep) production would, as the Commission has recently shown, not be very great by planting on hill grassland, and we can certainly no longer afford the great areas of the Scottish Highlands now devoted to deer forest. Here we should like to see great forests of climax conifers developed and allowed to grow to maturity. Such forests might well be things of considerable beauty as well as of high economic value, and they would develop an ecology, a flora and fauna of their own, of the greatest interest to plant and animal ecologists and to all naturalists. At the same time the now scanty remnants of old native oak, pine and birch wood in the Highland glens should be preserved as they are, and an effort made to induce natural regeneration by excluding grazing animals. Some of the most picturesque moorland and mountain country should, of course, also be preserved in its present state, but much of this is in fact 'unplantable'.

On the heathland of the English sandy soils, especially in Breckland, the Commission also has large plantations, and there is no doubt that this land is in every way suitable for the growing of conifers. Ecologists would, however, plead for the preservation of some of the best areas of heath in their open state, for example, in Breckland itself and on some of the Dorset heaths, because they support an exceptionally interesting flora and fauna which is profoundly modified or destroyed by planting. Agreement on the delimitation of them should not be difficult.

In the concluding pages of his notable paper Sir Roy Robinson remarks that 'it would doubtless be possible to found a whole system of silviculture on the theory of the succession of vegetation. Clearly it would have to be of the nature of a selective system under which single trees or small groups only were felled, because that is the only way in which we can conceive the succession proceeding uninterruptedly.' And again, 'there is room in British silviculture for other methods than clear felling and replanting...here there is an opportunity to practise silviculture on lines which have hitherto been neglected.'

This is exactly what ecologists would like to see. A forest developing to maturity on natural lines is an object of the greatest importance for ecological study, while a single crop of conifers, or of any other trees for that matter, is of very limited interest. In the initiation of a new forest which is to be allowed to develop to maturity mixed planting is no doubt an important technique, and some of the ecological research I have suggested should certainly throw light on the factors involved in the mutual relations of the planted trees. In the later stages of development it might well be possible to obtain natural regeneration as selective felling proceeded. During the whole period, ecological study of the development of the trees, of the accompanying plants and animals, and of the soil, should be continuous and could not but result in important accessions to knowledge.

On the lines I have suggested the Forestry Commission would not only discharge its primary economic task, but could help to conserve our native British woodland and at the same time create new forest communities of surpassing interest.

Sir Roy L. Robinson. I am flattered that the Ecological Society should have thought it worth while to pin to-day's discussion on my paper. Particularly do I wish to thank Professor Tansley for the comprehensive and sympathetic manner in which he has opened the proceedings. This is an opportunity for ecologists and foresters to make better contacts which I trust will produce useful results.

Perhaps you will forgive a personal aside. I am not a botanist much less an ecologist, and the paper was written by a forester for foresters. It has been my privilege to be in British State forestry from the jump, that is, counting the very tentative beginnings, upwards of thirty years. Some of my friends suggested, too kindly perhaps, that I must have learned something which would be of use to future foresters and that I ought to write it down. Having regard to the current uncertainty to life there was a case for making a record, but the more I looked at it the less I liked the idea. It seemed in fact that there were more urgent things to do and that time would not be available for doing what I would want to do.

There was, however, one leading consideration which has gradually forced its way into my mind, namely, the necessity of basing British forestry more squarely on Nature. Our first afforestation work was necessarily artificial in its main aspects. We selected and planted trees on the basis of such personal evidence as each of us possessed, confident even in some cases that our mere action was a warranty of success. It was not always so, and we had to set to work to find the causes of immediate failures. I do not regret that procedure. It has given us large areas of productive plantations, and it has also forced us to seek solutions to problems which we would not even have tackled had we played wholly for safety. It has also given us a practical view of the value of research and experiment in such an undertaking as large-scale forestry.

The main conclusion at which I arrive in approaching the sere and yellow leaf is that the processes involved in growing timber are far more interdependent than I had ever suspected. I am speaking now of the biological and not the physical aspects of managing forests. I take it that these interactions of plants, animals, and insects within the house, which is the forest, are the province of ecology in its widest sense. Therefore the forester, who has many routine calls on his time and energies, must seek the help of the ecologist.

Coming now to the substance of my own paper, I apologize, as I have already indicated, to your Society for its amateurish lay-out and at the same time venture to express the hope that you will both subject it to such criticism as it deserves and also, to the extent which you see fit, furnish us foresters with constructive proposals.

It has been suggested that because we seem to be in a fair way to solving the difficulties in establishing plantations on difficult sites we should be content to have achieved the result and not inquire into the reasons why. I feel that that attitude is short-sighted. It is improbable in the first place that we have extracted the last ounce of usefulness even so far as establishment of plantations is concerned, and I feel quite sure that what is useful in the establishment stages may also be found useful in the pole and semi-mature stages of forest crops.

It is possible too that by pursuing the ecological problems we shall get unexpected light on other problems. I have in mind particularly the problems of forest soil science. Here the agricultural approach has proved singularly inadequate. We have been groping for a long time to find a better avenue, and if the ecological holds out prospects, as I think it does, then we certainly ought to follow it up. Such an investigation would have to be comprehensive, calling for co-ordinated effort by ecologists, soil chemists and physicists, with the initial emphasis on the ecologists.

There is, of course, scope for much useful field work of a general observational character. The pine remnants of the Caledonian Forest present an interesting problem. Portions of it have now been kept relatively free of grazing for a number of years, and it is possible that useful information is accruing.

The selective felling, amounting often to devastation, which our broad-leaved woodlands are now undergoing is setting a very difficult reconstruction problem for the forester. Some better way than clear-felling and replanting at prohibitive cost must be found if possible. If we knew clearly the natural development of such areas we should be in a better position to regenerate them.

There is one other problem of general interest to which I would like to refer, namely, mixed as opposed to pure planting on sites other than difficult ones such as those to which my paper refers. Pure plantations are undoubtedly unnatural or at least highly artificial, and we are told that they may well lead to disaster through insects or other causes and lead also to soil exhaustion. It may be so, but we have to remember that some of our pure plantations are producing timber at a very high rate—200–250 cu. ft.

per acre per annum—which is a vital consideration in view of the necessity of recreating our reserve of standing timber in the shortest possible time. Others tell us that associations of pure conifers of various species will likewise lead to trouble, notwithstanding that the magnificent forests of western America are predominantly or wholly conifers. According to these authorities the admixture of quite a small proportion of broad-leaved trees such as birch or beech will put matters right. It may be so, but apart from the impossibility of getting any broad-leaved species to live for any appreciable part of the rotation in mixture with rapidly growing conifers I have an uneasy feeling that much of the argument is not based on observed facts which are strictly applicable to British conditions. This is a matter of some importance. If, as seems inevitable, we plant pure on a large scale, we ought at least to begin to provide our successors with the data on which to decide the advisability of turning over to mixed forests on the second rotation.

I look forward to your remarks, and if the Chairman so permits would like to reply to some of the points which may be raised.

Professor H. G. Champion. As Steven reminded us in 1930,* some at least of the general principles of plant ecology have long been recognized and often acted on in forestry, so that the modern science owes a considerable debt to silviculture. The paper now under consideration focuses our attention on the considerable development of ecological science and the help which might and should now be derived from it, in forestry operations.

The ecological approach has been more and more used in Indian forestry during the past thirty years at least, largely in relation to policy with regard to the effects of fire protection on the regeneration of the varied types of forest, sometimes found to be in the directions desired by foresters, but sometimes not. It was more specifically emphasized and expressed by a special committee appointed in 1933 to report† on the position in the *sal* (*Shorea robusta*) forests which extend over a tract some 800 miles by 200 miles in northern India. This committee, after extensive inspection and discussion, found that the ecological conditions in these sal-bearing forests varied so widely that the consequences of any particular operation carried out in any one of thirteen main types, and probably twenty-one subtypes, could not safely be assumed to be the same in any other, and as with fire protection, were already known to be different. May not something of the sort hold for the oak woods of Britain? In considering any forest type, the importance of determining its ecological status with regard to climax vegetation, and its dependence for continued existence on controllable factors, was stressed as an essential first step towards sound silvicultural treatment and management. In this connexion, the ground flora required as much attention as the trees if any were present. Sir Roy's paper reminds us of the value of existing vegetation as an indication of the potentialities of a site for afforestation, but as Steven and others have pointed out, it is equally important to sound the warning that owing to the aggressiveness and adaptability of the plant *Calluna*, 'heather ground' may be any of several ecologically very different types with very different potentialities, some intrinsically good, some amenable to treatment, and some very intractable. For *sal*, some forms of grassland provide a closely comparable case.

Sir Roy's first generalized conception of 'accelerated succession', to be intelligently applied in the interests of forestry, postulates that we have knowledge of the normal succession. Sometimes a deduction from established principles may suffice, but often our knowledge is so incomplete that results may be very disappointing owing to lack of recognition of some influential but less understood factor at work. We therefore require to study the natural successions, possibly with varying amounts of manipulation of the site factors, such as drainage and soil working, which are practical possibilities in afforestation; soil and rooting conditions require study equally with the vegetation. The ecological reserves, in the establishment of which the preliminary steps have already been taken, provide the opportunities for such studies, but there is much work to be undertaken before we have an adequately documented history of the developments which take place on sites of different types. A considerable amount of work on these lines has already been done with *sal* in India in connexion with systematic experimentation on regeneration problems and, as mentioned, very wide differences have been recorded. A comment, not out of place on the present occasion, is that the work has been almost entirely left to the foresters with too many other duties to carry out, and the botanical ecologists and physiologists are not taking a large enough share of the burden. This I felt impelled to stress to botanists meeting at the Indian Science Congress in 1938, pointing out that the forests, as the climax vegetation of almost the entire subcontinent, had a big but almost unheeded claim on their attention.

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* *Forestry*, **4** (1930), p. 26.

† *Indian For. Rec.* **19**, pt. III.

Now from a study of the site concerned and our knowledge of general principles of succession with a given flora, we arrive at some conception of the ecological potentialities which constitute Sir Roy's 'silvicultural stream', i.e. the lines on which the vegetation tends to move from its own interactions with the habitat factors. I feel, however, that there is a danger of over-simplification which should be kept in mind and can be illustrated from tropical experience. Just as we are tending to change Darwin's concept of the *origin* of species to the *origins* of species, so here it may be more advisable to bear in mind the probability that the stream may have several channels; it may converge with many others or it may split up into divergent branches possibly all merging in the end as a delta does in the ocean, but also possibly continuing divergent, or even, as rivers have often done in the past, completely reversing their direction of flow. The course and speed of the stream can certainly be greatly influenced by the introduction or exclusion of such everyday operations as grazing, burning, fire protection and draining. Turning to ecological terminology, I think I might say that as my own experience of old world tropical forests has grown, I have come to realize how enormously greater has been and is the influence of biological factors on the vegetation than one thinks on first contacts: in Indian forests it is certainly far more usual to be dealing with a biologically conditioned preclimax than anything else. The deduction from these considerations is once again that to derive such benefit as may be possible from working with the silvicultural stream, we need to know a lot more about the stream, and that as the movements are rather slow, the sooner we start to find out the better. The complications consequent on the introduction of exotics, some of which like Norway spruce might easily have been present in our natural vegetation but for historical and geographical accidents, do indeed increase the uncertainties, but do not greatly alter the general picture.

The claim that operations which move with the silvicultural stream are more likely to succeed than those which go against it, is generally supported by Indian experience.

Thus the artificial introduction of the species of the next stage of a succession is more likely to succeed than that of other species of similar requirements to the existing species, or than that of the climax species.

For instance, in the Himalayan forests the position and extent of the transitions from oak to conifer or one conifer to another are considerably altered when the forests are fire protected and the change to the new equilibrium can be hastened by silvicultural operations facilitating it, e.g. by opening up the oak, its replacement by natural blue pine may be expedited, and similarly for planted deodar.

How much one can expedite matters will depend on local conditions. A good illustration of this is the far more rapid succession on new alluvium under the more favourable climatic conditions of Bengal in contrast to the same succession in the more westerly provinces with a much longer dry season. In the latter, *sal* appears unable to establish itself until a considerable depth of loamy soil has been built up, by which time the original single-generation pioneer species (*Dalbergia sissoo*) will have disappeared, whereas in the former, *sal* may get established while the *Dalbergia* is still present. There is little doubt that lack of humus and appropriate soil flora and fauna are primarily responsible for initial difficulties on many new alluvial deposits, and the forester must accept the fact that time must elapse before they can carry the more exacting species of later stages in the succession. The pioneer species are possessed of adaptations enabling them to cope with the deficiencies as exemplified by the prevalence of Leguminosae with nitrogen-fixing nodules—as in the *Dalbergia* and *Acacia arabica* of river alluvium, and in the *Casuarina* of coastal sands.

Secondary succession can usually be expedited much more effectively than the primary, but to an extent depending on the degree of deterioration of the site which has occurred. Thus after a new clearing or heavy felling, there may be difficulties with the immediate re-establishment of the original climax type, but provided habitat conditions are not permanently changed by the introduction of new factors such as burning or grazing, conditions are rapidly restored when the soil cover is once more complete. Soil-inoculation experiments have shown that in some instances at least, biological factors are directly involved.

In the Bengal *sal* tract, it was found that fire protection was sometimes itself adequate to bring about the complete displacement of 'elephant grass' by tree growth (*Macaranga**), but none of the attempts to establish *sal* under or among this pioneer tree growth have succeeded so far. It seems probable that a period must elapse before this becomes possible. Similar difficulties have been experienced in other types of *sal* forest in other provinces.

Again, a less exacting nurse crop may be necessary in felled tropical evergreen forest to get the climax evergreen species re-established, but whether naturally or artificially introduced, this nurse crop can soon be gradually removed, or will in due course be largely crowded out by the climax species. Such appears to be the case with the mixed evergreen forests of India, and the silvicultural practice developed has been to go with the stream by first providing such a nurse crop and then hastening its disappearance when the time is ripe.†

By further development of this conception, we might anticipate that secondary successions might sometimes be so rapid ('telescoped') as not to allow adequate time for fullest development of one stage before passing on to the next. This does appear to be the case when we introduce on a cleared forest site a pioneer species, for instance, the *Dalbergia* already mentioned on a *sal* area. At first, with plenty of room and light it may grow very vigorously, but long before attaining normal maturity conditions become unsuitable and it dies out; meanwhile, by the protection it gives to the slower *sal*, it may favour the regeneration of the latter.

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* *Indian For. Rec.*, Silviculture, **1**, pt. I, Pl. 20.

† *Indian For. Rec.*, Silviculture, **3**, pt. IV.

One may contrast with this what may happen if species are introduced which belong to communities requiring more favourable conditions of moisture, etc., than are naturally available on the site. Account also has to be taken over the limiting effects of occasional combination of unfavourable factors which may not occur for some years after the introduction. With thorough soil working and other assistance, an excellent start may be made and all may go very well indeed, until, with advancing age and size, requirements go up and finally cannot be met—with resultant rapid deterioration and ultimate failure. India has several large-scale illustrations of this in the attempted rehabilitation of ravine lands under severe climatic conditions.

Several cases might be specified in which attempts to raise trees in full light have failed, apparently through insect attack, e.g. several of the Meliaceae and *Chlorophora excelsa*. Is this failure due to trying to go against the stream? It may well be so, for these trees in nature tend to come up singly or in groups in shelter or shade of other trees, and there escape severe attack or at least survive, and silvicultural technique has perforce to follow the same lines, adopting mixtures or introduction by scattered underplanting.

Turning to the next problem, the choice among the potentialities of the site under consideration, we come to *the conflict between the naturally occurring and the economically desirable*. Movement with the silvicultural stream, i.e. towards the climax vegetation, may mean movement from an economically profitable to a less profitable or even non-paying type. This is strikingly illustrated by our increasing knowledge of the ecological status of the *sal* and teak-bearing forests of India. It can be asserted without fear of serious contradiction that, over important parts of the existing distribution of these forests, they are not climax types; which latter would have little or none of these commercially valuable timbers in them, and instead, would consist mainly of species at present not marketable. Many of our best *sal* forests have almost certainly originated in heavy grassland formed after the clearing of mixed evergreen forest for cultivation and subsequent abandonment. Parallel illustrations could be drawn from other forest types in India and other parts of the tropics, notably the frequently higher commercial value of the trees of secondary or subclimatic semi-evergreen or moist deciduous forest compared with those of the climax rain-forest. The significance of this fact is that in such forests the forester's problem is to stem the silvicultural stream or perhaps to divert it. There are clear indications that to keep young *sal* plantations healthy in sites too damp for climax *sal* forest, they must be opened out and periodic ground fires must be run through them, season and severity depending on conditions.

Similarly in regeneration operations, expensively bought experience has shown that in moist types, drastic steps must be taken to reverse the current at least as far as the ground vegetation is concerned and force it back towards open grass and away from the natural tendency to close evergreen.

We know less about teak, but we are certainly not in the silvicultural stream at all with pure teak plantations, though systematic research work, particularly in Java, goes to show that they are by far the best economic proposition, not forgetting to take into consideration long-term reactions on soil productivity.* However, these complications only serve to underline the importance of ecological studies to chart the course of the silvicultural stream and to determine the effect on it of any controllable factors. In so far as the economic objectives lie at points along the main stream or such diversions, silvicultural operations with the current may be undertaken with much greater prospect of success than operations against it and may be expected to increase the velocity of flow.

A further example is available from the Himalayan coniferous forests where, as in Europe, the silver fir is the species best adapted to shade conditions and at certain elevations follows pure blue pine or mixed conifers including blue pine, deodar and spruce, the natural succession creating conditions in which the pine cannot regenerate as a crop, but only as scattered individuals or groups, whilst the fir is not easy to establish direct. This succession is very liable to be encouraged by normal regeneration operations, but unfortunately the fir is the least valuable species of all and often is either unsaleable or will not cover the costs of extraction.

In conclusion, it appears advisable to refer to the practical difficulty commonly experienced in India and the tropics (as in Britain!) in unconscious attempts to follow the silvicultural stream by planting mixtures. The end results have very generally been poor even where the start was good, but this verdict has been rather from the point of view of timber production than merely vegetative development. Just as the selection system, though perhaps the most 'natural' system, requires much more intensive management than the more artificial systems, so does the mixed plantation, though also more 'natural', require far more skilled attention than the single species plantation, and the poor results have mainly been due to lack of this attention. Greater knowledge is required of the natural tendencies of the components of the mixture and of the consequences of the manipulations open to the silviculturist and he must be constantly on the watch to control the silvicultural stream if he is to attain the best results. The probability is also that the form and nature of the mixture or final crop desired by the forester is decidedly different from what would develop if things were left to Nature.

Summary. Much of the progress of silvicultural practice which has taken place in the past thirty years has been due to the development of the ecological approach, as is best illustrated by the present position for *sal*, teak and Himalayan conifers. The importance of determining the ecological status of existing vegetation types is emphasized with a reminder that similar appearance may not imply similar status. Biotic factors have a very far-reaching influence on succession and must be taken into account. Instances of successful operations with the 'silvicultural stream' and resultant 'accelerated succession' are given from Indian forest practice as also of experience showing the limitations to which they are subject. Secondary succession offers greater opportunities than primary, presumably owing to soil differences and the process can sometimes be greatly telescoped. The raising of mixed crops introduces certain difficulties. The value of different species of timber bears no relation to its place in the natural succession and high commercial value of preclimax species may necessitate silvicultural practice definitely against the silvicultural stream, instances being given.

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* *Indian For. Rec.*, Silviculture, **5**, pt. I.

Dr A. S. Watt. In ecology, as in other branches of science, the dynamic approach has had a rich reward. Hitherto emphasis has been placed on plant succession—the sequence of plant communities in time at a given place, the general climate remaining constant. In true developmental succession the change is attributed to the action of the plants themselves, whereby one community so alters the total environment that it becomes relatively more favourable to some components of the next until ultimately a complex is built up in which climate, soil and vegetation are in equilibrium and remain in equilibrium only so long as the vegetation proper to it is maintained. In the plant successions with which we are immediately concerned the vegetation develops to a stage where trees first come in (the pioneers) to be followed by a series, short or long, of other species of dominant trees (successor species) ending in the climax, any one of these in Sir Roy's terminology being called a successor species. Our immediate problem is the relation between pioneer and successor, but in ecological theory any dominant in the series may play pioneer to the next dominant. The basis of the problem is thus broadened to embrace the relation between any two successive dominants.

Although in this country the general trend in plant succession is from habitats of extreme wetness or extreme dryness to mean moisture conditions, and from xerophytes and hydrophytes to mesophytes the actual mechanism by which the entry and establishment of one dominant in the community of its predecessor are secured may not primarily be connected with the relation of the plant to moisture. Thus in the succession on eroded sand in Breckland, *Cetraria aculeata* follows *Polytrichum piliferum* because the latter provides a suitable physical anchorage: and in the hydrosere in fen, *Cladium mariscus* invades reed swamp when the accumulated organic matter causes the shallowing of the water to a point where adequate supplies of oxygen, entering the part of the leaf above water, are maintained to the growing parts of the plant below water. In both of these examples the entry and establishment of the successor species would seem to have a purely physical basis.

Considering next the order in which the dominants occur we may take the succession on the South Downs as an example. There, if the three species ash, oak and beech start level, there will in time be a fractional separation into ashwoods, ash-oakwoods and beechwoods. This separation is primarily an expression of a gradient in mobility aided by gradients in abundance of seed and earliness and frequency of its production and conditioned by the gradient in light demand and the sensitiveness of the seedling to frost. Here beech can invade the woods of ash and oak, receiving adequate light intensity in mature woods and protection from frost: in other words, it is adapted to the microclimate of these woods. The microclimate of scrub at certain stages of its development is equally suitable. Furthermore, cover, although desirable, is not always necessary and beech can invade grassland directly. Thus conditions suitable for beech establishment are found over the whole range of habitats represented by grassland, scrub, ash and ash-oakwood. There is no need to postulate soil preparation or direct or indirect root action. That does not mean to say these do not exist or there is not an influence which is favourable but merely that the succession can be adequately accounted for in terms of the general biological equipment of the species without reference to any more specific relation between the successive dominants.

In the foregoing I have taken the South Downs as a whole with ash as the general pioneer tree, but there are places—the most exposed places facing south-west—where the relations between ash and beech are reversed. In these exposed places beech is the pioneer and ash the successor in so far as the establishment and growth of the beech provides conditions suitable for the entry and successful growth of the ash.

The number of wood-forming species in this country is so small that the species we have form woods over a wider range of habitat than they would had they to meet with competition from other species better adapted to parts of it; moreover, some form the climax simply because other life forms proper to the habitat have been exterminated during the last ice age or have not returned. The consequence is that our tree successions are short and provide only some of the data on which generalizations can be made about the contrast between the characteristics of pioneer trees and the climax species. Moreover, natural selection (including selection by the vegetation itself) has led to the survival of species with certain combinations of characters which fit the species for the part they play in succession. In general (and there are many exceptions in detail) pioneer trees of the xerosere are frost-hardy, light-demanding xerophytes, non-exacting as to soil, deep-rooting or accommodating, insensitive to oxygen supply in the soil and mobile. Successor trees and climax trees in particular are frost-sensitive, shade-bearing mesophytes, more exacting as to soil, shallow-rooting, sensitive to oxygen supply and immobile. The outstanding fact about those species which act as successful pioneers in planting—the pines and birch—is that they have most of the attributes of pioneers: moreover, they grow in a wide range of climatic conditions and play pioneer to different successors in different climates. This again would seem to exclude any specific relation between pioneer and successor.

Before considering Sir Roy's data in the light of these remarks may I point out that the critical phases for succession in the life history of a plant may be the germination of the seed and the establishment of the seedling. These are exactly the phases which are passed in the favourable conditions of the nursery. Nevertheless, a plant may retain some of its juvenile features for some years beyond the age of the transplant. Further, the plant which is put out in the field is not the same as a plant of the same size grown from seed on the spot, in particular the form of its root system is different, being fibrous, compact and shallower. In fact the plant may be deprived of its main equipment for survival.

The evidence presented by Sir Roy seems to me fully to justify the practice of using a pioneer with a successor where a successor crop is desired. But how far this practice should be extended and what conjunction of species should be used, should depend on an appreciation of how the pioneer acts. From what has been said already there is likely to be more than one cause at work, and the several causes may be operative to different degrees in different habitats.

In the investigation of cause I should put in the forefront an analysis of the microclimate. The data from Breckland about the response of Douglas fir five years after mixing with pine are capable of an interpretation in terms of a change in the microclimate: protection from frost and from drying winds only after the pines were of a size to provide it would seem to afford adequate explanation. The extension of the influence of the pioneer to pure crops of the successor both to windward and to leeward could be explained on the same basis, for, as Russian data on the effect of shelterbelts show, the wind velocity is less both to windward and leeward than it is over the open steppe. Also the mingling of warmer air from a plantation with the colder air outside means that at ground level during frosts there is a fall in temperature from the plantation outwards, and between plantations the blanket of cold air would be thickest in the middle and thin out towards the plantations on each side.

If there is anything in what I have said, then in areas where the microclimatic factor is important the amelioration of the local climate however caused would produce similar results. Thus a sufficient body of taller growing successor individuals in a plantation generally in check would act as a nucleus of amelioration, its influence extending beyond its limits and gradually spreading outwards. Again the successful establishment of any woody species, whether shrub or tree, provided it had the same ameliorative influence as pine, ought to give similar results. From none of these, however, is root action excluded. On the other hand, the shelter provided by a stone wall should produce similar results, and the extension of the idea to the use of hurdles or canvas between the rows of trees is suggested for experiment with the observation that they would not afford the same kind and degree of protection as that afforded by spreading trees. In an anticyclonic inversion protection would be negligible: but a light cover over the top together with side protection would provide the necessary experimental technique for finding out whether death or check in the successor was due to microclimatic causes. The primary need is to ascertain the cause of death or check.

In saying all this I am not arguing that the microclimatic factor affords a full explanation of the effect of the pioneer on the successor. I merely wish to point out that no convincing case has been made out for excluding it. On the contrary, in my judgement there is a prima facie case for its fuller investigation.

Soils. In a virgin succession there is an increase in productivity with time, and in the climate of the region of brown earth soils the maximum productivity is reached near the climax. In podsol regions, however, the peak of productivity is probably attained at some distance short of the climax, and it is at least doubtful if the postulated relations between pioneer and successor hold. With virgin successions, however, we have little if anything to do, for the bulk if not all of the plantable land in this country has at some time or other carried woodland (not necessarily close-canopy woodland) and consequently belongs to deflected successions. The soils of these deflected successions differ in greater or lesser degree from the woodland soils from which they were derived and do not therefore necessarily present the same problems as in virgin successions. Some soils as those on the South Downs retain sufficient of the major properties of woodland soils to be colonizable by trees whether pioneers or successors. Ash, although a pioneer in the deflected succession as already described, lacks some of the critical attributes of a pioneer and may not have been the pioneer in the virgin succession. In fact, I have for some years held the view, unsupported though it is by archaeological evidence, but backed by a considerable body of ecological data, that pine may have been a pioneer in the virgin succession on highly calcareous soils. Its usefulness in the establishment of beech was therefore not unexpected, and the need for a pioneer in plantations is quite compatible with the fact that beech may invade chalk grassland directly without the aid of a protective cover.

Besides these soils which retain the major properties of woodland soils there are others which show all grades of change to extreme types so altered by erosion or waterlogging and peat formation that they no longer belong to the category of plantable soils. There are, however, in the intermediate grades large areas where the change has been less extreme with soils which retain the skeletal attributes of woodland soils such as depth, but whose texture and base status have been altered. These in the main are the direct or indirect result of human interference in the past, and the forester's task is not only to plant trees but to build again the old waste places so that they will in time be able to carry a crop of trees. Viewed thus the forester's work calls for considerable patience and forbearance: his problems are also a challenge to man to restore to fertility the man-made wastes.

The building up of soils is in great part the work of plants, and for the continuation of the process there must be continuity in the plant succession, that is a series of dominants with interlocking requirements must be present. If through any cause the necessary dominant is absent the stage in succession reached will not necessarily stay at that level but retrogression may set in. This may occur at different stages in the succession. Thus in the absence of a sufficient binding force of grasses, the succession on eroded sand in the Breck reaches as far as a mixture of dominant *Cetraria-Cladonia* which on the decay of the anchoring *Polytrichum* disrupts, the soil is exposed and through wind erosion the built-up soil blown away exposing once again the erosion pavement from which the succession started. Again at a higher level in the hydrosere, as in lakes, plant remains may be accumulated to a point where *Phragmites* should come in. In its absence the existing plant community, by further accumulation of organic matter, makes the habitat worse for itself and in time is no longer able to hold the ground: the accumulated soil is eroded and the succession starts at a lower level. Similar examples are found in peat both in the raised bog and in blanket bog. At a still higher stage, and one of particular interest to us, destroyed woodland has been replaced over wide areas by *Calluna* which, through its highly dispersed acid humus, accelerates podsolization. In extreme cases as in parts of the Breck this process has gone to a point where the soil and vegetation no longer form a stable system: the podsol is broken down and its component parts dispersed by wind to form the material for a fresh start. This is one of Nature's ways of restoring the position created by her insurgent son.

In slightly less extreme cases, as at Wareham, the retrogression has not gone so far, yet far enough to make even the establishment of a pioneer difficult. In most areas the establishment of a pioneer is possible, and by its aid a successor may achieve success. The problem at issue is how.

The effect of trees on the soil of such *Calluna* areas has not, so far as I am aware, been the subject of inquiry: and on the general problem of the changes in soil wrought by scrub and by forest there is little exact information from areas in this country. The unpublished work of Ross on the effect of scrub on the heavy chalky boulder clay west of Cambridge confirms the general opinion that the texture of the soil is altered. Whether this alone is sufficient to account for the success of the successor or whether other and more subtle changes are brought about needs further investigation. This however can be said, that anything, be it texture or aeration, which favours the absorption transpiration balance in the transplant will help the trees. To that extent at least the condition of the soil is important, and woodland soil is generally in a better physical condition than soil under *Calluna* when the pine and birch, which are less sensitive to oxygen, have a greater chance of successful establishment than the more sensitive climax species. On this point one would like to see or hear of experiments on the effect of the pioneer on the successor on contiguous areas with woodland and non-woodland soils respectively, where it can be demonstrated that the microclimatic factor and the vegetational or biotic factor are the same.

The relation of one plant to another. The subject of the relation of one plant to another raises issues too vast to be discussed in detail. Broadly the relations may be classed as dependent, competitive or mutually beneficial. The relation between plants is not always in one category: a tree may provide shade and shelter to its dependent and yet compete with it through its roots: the relation between legumes and grasses is both mutually beneficial and competitive: the relation between a fungus and its host in mycorrhiza may be all three. It seems to me therefore to prejudge the issue of the relation between pine, say, and spruce by writing it down as always competitive. Such relations are usually dependent on the conditions, and I see nothing inconsistent in the view that young pine on *Calluna* ground may be beneficial to young spruce, while on other soils and at other ages the relation may be competitive. Grass on the floor of a wood depresses the growth of ash: beech, so far as I know, is not similarly affected: in a mixture, beech, by killing out the grass, will *in that way* favour the ash. Similarly, pine is a normal invader of *Calluna* heath: by killing the *Calluna* even partially root competition between spruce and *Calluna* would be reduced. Nor can we exclude even more subtle relations: the annual shedding of mycorrhiza by pine may provide suitable nutriment to spruce, and even the dead roots of *Calluna* may do this. And the further possibility exists of direct action through root excretion. The significant association in the Californian Desert between certain species of annuals and certain species of shrubs, alive, dead or decayed, provides an example of an intimacy which suggests some chemical action. Our ignorance of such matters is, however, fairly complete.

The problem of mixtures as distinct from problems of establishment raises other issues. The claim that a mixture of deep-rooting and shallow-rooting trees has a higher yield may be valid. Dredge corn (a mixture of oats and barley) is claimed by its growers to produce a higher yield than either of its components. The claim, however, has never been substantiated by experiment and the issues involved are complex: the relation between the components may be complementary nutritional, the direct action of one kind of root on another, or microbiological. Similarly, the vertical stratification of the roots and shoots of species in the different layers of a wood may reduce competition but does not exclude it. This raises the whole question of the structure of a plant community.

The structure of the plant community. I began by pointing out that the dynamic concept had been successfully applied in the interpretation of vegetation as a whole. I should like now to consider its extension to the plant community itself and to show, first, that the phenomena of the plant community are essentially of the same kind as the phenomena of plant succession, that is, the relations between components of the plant community are dynamic and based on the reactions of the plants themselves: and secondly, that many of the foresters' difficulties result from the non-natural, man-made structure of much of our vegetation.

On the better soils of the Chiltern plateau birch plays pioneer to the successor beech (the intermediate stages may be omitted for simple treatment). On such soils the struggle between them is a foregone conclusion: the light-demanding and small birch is no match for the tall shade-bearing beech. Inside the beechwood the beech regenerates without the aid of birch. On the other hand, on the poorest soils beech loses its advantage of height, and failing to reproduce under its own canopy gaps are formed in which birch plays the part of pioneer. Under the birch the surface soil is changed from a mor condition to something near a mull: beech comes in, and growing under the birch finally prevents birch from reproducing in that place. The same cycle is repeated in other gaps and the wood taken as a whole is a stable birch-beech wood, in which at any given time the proportion of birch to beech may vary, but birch will always be a constituent and one perhaps necessary to the continued existence of the beech. Thus the scales which, on the better soils, are heavily weighted in favour of the beech so that succession takes place are on the poor soils more evenly balanced, the progressive component of change leading to succession being effectively offset by the inability of the beech to maintain continuity in space and in time over the whole area. The two phenomena, namely, plant succession and the internal cycle of change, are the same in principle. And although it may be convenient to treat them separately the establishment of woods by mixing pioneers and successors and the maintenance of mixtures in plantations rest on the same kind of natural process.

Next compare the pattern of an even-aged pure plantation (i.e. a crop) with a natural forest or with its nearest equivalent under management, the natural selection forest. In the life history of an even-aged pure plantation there is a definite sequence of change in time. As the trees grow the number per unit area falls, their power to exclude invading species also falls and subsidiary vegetation makes its appearance, marking stages in the life history of the plantation. Thus in certain Scottish pinewoods the absence of ground vegetation following the formation of canopy is followed by the succession of dominants, *Deschampsia flexuosa*, *Vaccinium myrtillus* and *Calluna vulgaris*. Denoting these stages by the numbers 1–4 we have the scheme on the left showing the distribution of the stages in space and the change in time. Compare this with a pinewood managed on the selection system (scheme on the right):

Change in time

4	4	4	4
3	3	3	3
2	2	2	2
1	1	1	1

Distribution in space

The even-aged plantation

Change in time

4	1	2	3
3	4	1	2
2	3	4	1
1	2	3	4

Distribution in space

The natural selection forest

At any given time there is a patchwork of ground vegetation representative of all phases in the life history and related to the competitive power of the trees. Also at any given place in time there is the sequence of change found in the even-aged plantation. The selection forest illustrates the dynamic pattern or cycle of change, the minimum time required for its completion being the length of the rotation.

Now consider the relation of these systems to an invading species of tree. Unless the species comes in at the beginning, that is with the dominant, its successful establishment in the even-aged wood will have to wait until such time as the competitive power of the dominant is reduced with opening up of the wood; let us say until stage 4. In the selection forest, on the other hand, the invader can immediately become established in those places at no. 4 stage: and since in time every part of the wood will pass through that stage the invading species will have an opportunity of invading each part of the wood. Whether the invasion will lead to succession or to a stable mixed wood will depend on the relative competitive power of the species under the given set of conditions.

Because it is regularly burned the Callunetum as commonly seen in this country has the structure of a crop or an even-aged pure plantation. An invading species may come in at the beginning after burning, but in the 'tight' heather stage difficulties are presented just as in the middle stages of the plantation, and it is only when the heather becomes old and leggy that a further opportunity is given. This does not usually happen because of burning before that stage is reached. Unburned heather, however, shows a structure comparable with that of a selection forest: it is uneven-aged and shows a dynamic pattern with old leggy or stick heather appearing at intervals. These are the invasion points for pine, that is, places where the old and dying heather no longer presents the same level of competitive power. Again, just as in the selection forest, the whole area is capable of being invaded by pine, and the minimum time required is the length of life of heather in this country, namely, about twenty-five years.

Much of the so-called natural vegetation of the country has this crop structure. Scrub may be so dense on the ground that its invasion by trees is impossible until with age it opens out, the uniform crop-like structure arising from a sudden release from grazing or from arable cultivation. The 'tight' stage in yewwoods may last several hundred years before the wood opens out to allow the entry of invading species. The bulk of our broad-leaved woods have this crop structure consisting of grandparents without issue. Grassland previously grazed and then enclosed against rabbits shows a uniformity and competitive power arising from its crop structure which increases the difficulties of establishing trees. To give the devil his due, the rabbit is not 100% hostile. Left to themselves all these types of vegetation would in time show a natural as opposed to a crop or artificial structure. This is not to be interpreted as an argument for delay in planting: I am merely trying to outline the framework within which explanations of the forester's difficulties may be looked for.

The problem of mixtures has engaged the attention of foresters for a long time, and in their understanding of the relations of one species of tree to another forestry practice is ahead of ecological theory. By determining the kind of dispersion which species show in a plant community Dr Clapham and Dr Blackman have made a first attack by statistical methods on the problems presented by its structure. The next step is to find out how species are related to each other. This has been done for a number of plant communities whose structure is relatively simple, and the data show that the same fundamental relations as seen in the natural selection forest, whether it consists of one species of tree or more, hold for the non-woodland community as well. In other words, there is on the ground at any given time a pattern, like the pattern of a carpet or a wallpaper, but unlike these the pattern is dynamic, the components moving from place to place in time but always showing the same basic relation to each other. The recognition of this pattern and the study of the relations of the species composing it are of primary importance, and to my mind constitute the most urgent single problem in what may be called straight ecology. It even raises the fundamental issue of what constitutes a plant community. In his essay on the poems of Robert Montgomery, Macaulay makes some remarks apposite to this issue. 'His writing bears the same relation to poetry which a

Turkey carpet bears to a picture. There are colours in the Turkey carpet out of which a picture might be made. There are words in Mr Montgomery's writing which, when disposed in certain orders and combinations, have made, and will again make, good poetry. But, as they now stand, they seem to be put together on principle in such a manner as to give no image of anything "in the heavens above, or in the earth beneath, or in the waters under the earth".' In other words you may bring together the elements of forest from divers sources and yet not make a forest. A good forest must be racy of the total environment including the relations between its members.

Further, it is not merely a question of the association or grouping of species selected by the organic and inorganic environment, but of the way in which the species and individuals of the species are put together to form a pattern in space and in time—'their disposition in certain orders and combinations'. There are really two components to this problem, the proportion of one species to another and the way in which the species are associated. For example, fescue-bent pastures show all transitions from pasture with abundant fescue and negligible bent to abundant bent and negligible fescue, that is, the proportions of the species vary. As yet we do not know what factors determine the numerical relations of these species. But there is the further question, to which there is also as yet no answer, of the pattern which they make or the way in which they are put together. Put in its simplest form the problem in a mixed plantation may be represented by a comparison between the stem for stem mixture and the line for line mixture. In the diagram

$$\begin{array}{cccc} a & b & a & \cdots \\ b & a & b & \cdots \\ a & b & a & \cdots \\ \vdots & \vdots & \vdots & \end{array}$$

stem for stem mixture

$$\begin{array}{cccc} a & b & a & \cdots \\ a & b & a & \cdots \\ a & b & a & \cdots \\ \vdots & \vdots & \vdots & \end{array}$$

line for line mixture

the proportions of the two species are the same, but the record of density takes no account of the relative position of the species, for in the stem for stem mixture a's nearest neighbours are four b's and in the line for line mixture $2a+2b$. Thus the two systems are not the same. And this raises the further question of the size of the unit in the dynamic pattern: in some habitats a mixture of two species may succeed as a stem for stem mixture, in other habitats for the best results the same two species ought to be planted in groups and in groups of different sizes according to the habitat.

These ideas are more familiar to foresters than to ecologists. Ecologists in fact have a long way to go before they know enough about the relations between species in the plant community to make generalizations which will be useful in the practice of forestry, and to achieve this desirable goal much more intensive study of the static and dynamic structure of the plant community is needed. The same holds good in the diagnosis and delimitation of plant communities: the forester can diagnose Callunetum as easily as the ecologist: but there are *heaths* and *heaths*, and to be of real service the ecologist must in his systematic work on plant communities be a 'splitter' and not a 'lumper'. Here again pattern as a criterion will be of service.

Professor Tansley's *Vegetation of the British Isles* is a landmark. It is the climax of a phase in which the main theme has been the relation of one plant community to another. The next stage, in my view, will be the intensive study and elucidation of the dynamic relations which hold between one species and another in the plant community itself. The establishment of generalizations based on information of this kind, and the focusing of these on the special problems of the forest, should be to the mutual advantage of the forester and the ecologist.

Professor H. M. Steven. It may be useful to mention what ecological studies are of special value and interest to foresters. Apart from vegetation, both ecologists and foresters are particularly concerned with factors of locality. As ecology passes from the descriptive to the experimental phase this common ground will extend.

Experience of afforestation in this country has shown the importance of a close study of climatic factors both general and microclimatic. Although the study of ground vegetation types has proved of great assistance in afforestation, soil profiles when properly understood may be expected to give even greater assistance, because therein was reflected the past history of the site and the reaction of its vegetation over a long period. Each soil type had characteristics of value in deciding silvicultural technique. Of paramount importance, however, was the nature of the leaf litter and humus. In the formation of plantations the nature of the leaf detritus of the ground herbage plants, and the species from which it was derived, affected tree species in different ways, and was at least one cause of the behaviour of pioneer and successor species. It, therefore, affected choice of tree species and mixtures. Later it influenced thinning technique, and was of critical importance in systems of natural vegetation. Indeed, the whole of silviculture may be viewed from this point of view.

Secondly, the ecological concept of climax was of importance in afforestation in this country. If certain upland heaths and peat lands were edaphic climaxes as envisaged at one time by Professor Tansley, then their successful afforestation would meet even greater difficulties than had been encountered to date.

Coming to the concept of succession, it would undoubtedly be of great value in silviculture if ecologists could work out in greater detail the mechanism of the reaction of seral stages in improving the habitat. This knowledge would have wide application. Mixtures of hardy tolerant pioneers with successor species may not prove successful on the most difficult sites, e.g. probable edaphic non-woodland climaxes. It may be necessary to have pure crops of the pioneers as well as special soil cultivation technique, introducing the more valuable successor species at a later stage.

Finally, the reaction of a community on the soil type is of vital importance from the point of view of the maintenance of soil fertility. In this connexion has the preponderance of light-demanding species in the natural woodland communities of this country any ecological significance?

Dr L. Dudley Stamp. Dr L. Dudley Stamp said he was particularly interested in the discussion as it affected the broader issues of national land planning. Reference had been made to the very varied physical environments of our relatively small country, and there was need of detailed study that full use might be made of all types of land in the national interest. Expressed in simple terms the land must satisfy five of the major needs of the people—land for industry, for housing, for food, for raw materials (including timber), and last but not least for recreation in the broadest sense—refreshment for mind and body. Since it was true that our climate is essentially a forest climate and that woodland was the climatic climax vegetation of most of the surface, there was danger of a competition between afforestation and other uses. Unfortunately, it was true that the competition between industry, housing and agriculture was fiercest for the *best* land—level or undulating, well-drained land equally suitable for 'development' as for farming and, it must be admitted, for forestry. The danger disappeared if forestry were made the solution for the use of the poorer land of the country, and if Professor Tansley's concept were accepted, that afforestation was primarily a matter for what geographers call 'Highland Britain'—the old-rock massifs of the west and north. Public opinion was conservative and needed to be educated to the realization that this country could, if it liked, possess something of the stately charm of the Black Forest, the fairy quality of the Finnish forests sprinkled with birch and aspen or even the incomparable majesty of the Californian Redwood Highway. The vision seemed particularly attractive for the Scottish Highlands, where at present virtually uninhabited Deer Forests covered nearly a fifth of the whole country and where it could not be said that the hill sheep had a prior claim, since only 3 % of Scottish hill sheep grazed in the Deer Forests.

Was it possible that the ecologist held the essential key to the problem of the best use of land, especially hill land? Broadly speaking rough grazing—land agriculturally submarginal—covers some 18,000,000 acres or a third of England, Wales and Scotland; the areas which it covers are shown on the new maps of land utilization (recently printed by the Ordnance Survey in two sheets on the scale of 1:675,000 for the Land Utilization Survey of Britain and the Ministry of Town and Country Planning) which were exhibited, and the character of the rough grazing was shown for England and Wales in Stapledon's Grassland Survey, of which a coloured MS. copy on the same scale was exhibited. Armed with such maps and his knowledge of the succession, could the ecologist delineate those areas where grassland improvement was the best course in the national interest and others where afforestation should be paramount? There did seem to be a possibility that tracts would remain—for example of Eriophoretum—which nobody would want, though such might be the essentially remote tracts needed for nature reserves. Referring to a possible competition between hill-sheep farming (so essential for the maintenance of our live-stock industry) and forestry, there seemed to be the problem of the unplantable land: whilst the productive value of *part* of a tract of hill land was being raised by planting, that of the remainder was being lowered, since it was neither plantable nor, as left, useful for sheep.

The speaker hoped that ecologists would play a major part, in the first instance through a nation-wide survey, in the determination of a balanced use of the nation's land resources. There was need for the practice of the old-fashioned virtue of thrift; there was nothing incompatible between proper use of land and what is usually called its 'amenity' value, and only by properly planned use should we secure the conservation of adequate tracts where the indigenous flora and fauna could still exist.

Mr J. McDonald. Mr J. McDonald said, there is a danger that the problems facing the forester may be oversimplified. The concept of the silvicultural stream must take account of the fact that such streams vary in speed and even in direction of flow. On the chalky Boulder Clay of Lincolnshire, for instance, the movement towards forest is very much faster than it is on the Bunter Sands of Sherwood Forest. In relation to broad-leaved woodland, while the climax types of tree in this country may constitute forest to the ecologist, to the forester they are woods not worth their keep—as, for instance, oak on dry acidic soils. Can the ecologist tell then, how forestry can be made productive without planting conifers?

With regard to the scarcity of shade bearers in the country, referred to by Professor Steven, some of this at least may be due to the influence of the game preserver, either in cutting out, or in refraining from planting, heavy shades, with a view to the conservation of ground cover.

Professor Tansley had referred to study of the autecology of exotic conifers. While agreeing that more extensive knowledge is needed here, it may be suggested also that we require information about such native trees as will mix readily in plantations; e.g. lime is well worth keeping, and, at least in the Midlands, it mixes well. Foresters, however, know very little about our native trees. They do know that wych elm and sycamore grow well. But where should they be put?

The reconstruction of our broad-leaved woodlands has been sadly neglected. Professor Champion has recommended protection. This may help, but only on the better soils. A recasting of the future training of foresters and forest officers, with an increased weight of emphasis on ecology, will also lead to a solution of this and many other problems.

Mr W. H. Guillebaud. Mr Guillebaud, speaking as Chief Research Officer of the Forestry Commission, agreed with Professor Tansley's statement as to the need for studies on the autecology of the more recently introduced exotic species of forest trees, and referred to the numerous experimental areas laid down by the Research Branch. These areas contained comparable plots of many of the exotic species. The Research Officers would welcome any opportunity of showing these experiments to ecologists who might be interested in this problem.

A little further light has been thrown on the nature of the changes produced by the growth of the pine in the pine/spruce mixtures referred to in Sir Roy Robinson's paper. Observations at Teindland, by Dr A. Muir of the Macaulay Institute of Soil Research, show that one effect of the pine is to produce a thin but well-defined layer of black raw humus on the surface of the soil, and that in this layer the finer spruce rootlets are strongly developed. Where there is no pine with the spruce the peat is undecomposed and of a greasy texture and there is no superficial layer of raw humus. In another experimental area in Scotland plots of pure spruce adjoin plots of Scots pine and of Japanese larch, and the two or three rows of spruce next the pine or larch show greatly improved growth compared with the spruce in the rest of the plot. Dissection of the roots of some of the spruce shows that the roots of the trees in the penultimate row are markedly longer and stouter in the direction of the larch or pine than they are in any other direction. Both the above observations show that whatever benefit the pine may confer in the form of shelter, there is also an edaphic effect of considerable importance.

Graphs illustrating the development of the spruce in pure and in mixed plots at Teindland and Allerston experimental areas were demonstrated to the meeting.

Dr G. E. Blackman. It has been stated at this meeting that the agricultural approach, at least so far as soils are concerned, is a hindrance rather than a help in the consideration of forestry problems. It is therefore with some hesitancy that I venture to make suggestions as to the interrelationship between afforestation and ecology because I admit in part to an agricultural outlook.

As an ecologist with experience of agricultural research I am firmly convinced of the value and importance of statistics and statistical methods in the solution of agricultural problems. I am equally convinced of the importance of the same methods for autecological investigation, especially in woodland communities. This conviction is based not only on general grounds but also on the knowledge acquired over several years during investigations on the autecology of a woodland plant: a plant admittedly of no economic importance but with a high amenity value—the bluebell. By the application of statistical methods in field studies it was possible to establish that where the mean light intensity over the period March to June did not exceed 10% of daylight no bluebells existed. Furthermore, by conducting parallel experiments in the open, where plants were subject to varying degrees of artificial shading, it was found that no gain in weight took place below an intensity of one-tenth daylight. Thus the two sets of figures obtained by experimentation and by direct observation in the field are in good agreement.

I do not quote these figures for their intrinsic interest to foresters, but only to show that by controlled experiments, coupled with field studies, it has been possible to define precisely at what point light as one of the environmental factors of woodland will limit the establishment of the bluebell. There is, moreover, a further point. As far as I am aware accurate data of this nature are not known for any other woodland plant. Yet such information for tree seedlings must be of primary importance in problems connected with natural regeneration, and the degree of selective felling required to give optimal light intensities for the establishment of seedlings.

I do not wish to imply that investigations should be confined to the minimum light requirements of trees and other woodland plants, because with increasing light intensity other factors may become operative. There is, for example, evidence that under some American conditions the fall in moisture content associated with rising light intensity will determine the limits within which regeneration will take place. It cannot, however, be taken for granted that woodland species will necessarily grow best under the conditions of the woodland environment. In point of fact the bluebell has the highest growth rate in the open and is rarely found outside woodland in south and eastern England because of the competition for water with grasses and the damage caused by grazing animals. In the higher rainfall areas of the north and west, bluebells will grow in full daylight in localities where grazing is infrequent in the spring and the soil is not waterlogged. There are a number of other contributory factors which though they may play some part in determining the distribution are of minor importance and need not be discussed.

This information I have given for the bluebell will I think serve as an illustration of how it is possible to analyse with some precision the complex of environmental factors by combining detailed field studies with multifactorial experiments. The main point I here wish to make is that investigations along similar lines for both indigenous and exotic trees should go far to elucidate many forestry problems and make it possible to predict where tree growth would be satisfactory. Reverting again if I may to the bluebell as an illustration it can be stated that the replanting of clear-felled deciduous woodland with evergreen conifers will lead to the elimination of the bluebell, but that by mixed planting of deciduous and evergreen trees in proportions that can be calculated this elimination will not take place.

Sir Roy Robinson, in his discussion of the problems of accelerated succession, has stressed the importance of detailed observations in plantations set aside for ecological investigation. Of the value of such observations there is no doubt, but it seems to me that a full understanding of the successional changes taking place cannot be achieved by these means alone. In addition to these plantations new experimental plantings laid out in randomized blocks are required. The design of such experiments, since they must be essentially long term, will need careful thought and discussion between foresters and ecologists as to which factors are likely to be of most importance. One factor which must be investigated is the effect of varying the distance between the rows of the pioneer species on the growth and development of the intervening exotics.

Coupled with these large-scale trials other smaller experiments are required where the environmental factors can be changed experimentally. Such investigations must embrace direct measurements of growth and probably physiological changes, since, if the function of the pioneer species in mixed plantations is associated either with shelter or shade, then the effects may be extremely complex. From work now in progress at Imperial College it has been found that in annual plants a reduction of light intensity to half daylight increases the height, leaf area and the proportion of stem dry matter, decreases the root weight, net assimilation rate, but does not change the total plant weight. Moreover, the extent to which these alterations will occur can be widely affected by variations in the mineral nutrient level, and at different times in the season some trends may even be reversed. Whether tree seedlings will react in the same way as annual plants is unknown, but the sudden onset of extension growth of exotic conifers described in Sir Roy Robinson's article may be brought about only after some degree of shade has been established by pioneer *Pinus sylvestris*.

It may be thought that the programme of research as outlined is in scope and detail formidable, but so too are the problems concerned with the post-war afforestation. If these problems are to be in part solved in time to be of practical value during the next decade then the situation calls for co-ordination and intensive investigation by teams of workers. Primarily an ecological survey of Great Britain as suggested by Dr Stamp will be of great help, but as Professor Tansley has pointed out ecology is a young science, and I personally doubt whether the present state of existing knowledge is sufficient to foretell within narrow enough limits which localities or communities are suitable for tree planting. Ecologists would welcome the opportunity of extending their knowledge in this direction, but in the past they have been hampered by lack of numbers, facilities, field laboratories and finance. If these obstacles were removed then the advance of knowledge should be rapid enough to help solve the difficulties of the post-war programme of afforestation.

Dr M. C. Rayner. There is one aspect of forest ecology that I take this opportunity to stress. Except in relation to root diseases, I think that plant ecologists have tended to overlook—certainly to underrate—the importance of soil fungi in general as potential factors in the ecology of the higher plants. This is especially true of trees and particularly of certain groups.

My own views have recently tended to crystallize. I regard the mycorrhizal habit in trees as a specialized ecological relationship, the distribution and activity of the mycorrhiza-formers being closely bound up with the whole complex of biological soil activity in relation with the kind of humus substrate that is being formed. Under natural conditions, the establishment of balanced mycorrhizal relations is in itself a formal condition for healthy growth.

The members of certain groups of trees—Abietineae, Cupuliferae and others—show a multiple habit in respect to mycorrhizal association, and I think it likely that the capacity to form regular and stable root associations with a number of different species of soil fungi is in itself an ecological adaptation bound up directly with other edaphic factors.

In the establishment of a new ecological unit during afforestation, sometimes all goes well and the complicated biological soil factors become automatically adjusted to form a stabilized system.

Often there are difficulties, and we have learned that disturbance of edaphic relations is apt to be quickly reflected in mycorrhizal equipment, so that the incidence and structural features of mycorrhizas are a valuable index to the suitability or otherwise of soil conditions, and may be a useful guide to their modification.

In the case of trees, convincing evidence is now available as to the delicacy of these ecological adjustments and the sensitiveness of tree growth to their impact. For example, the disturbance of ecological balance that occurs after felling is quickly followed by an obvious shift in the fungus population. This, together with the change in the character of the organic detritus that reaches the soil, will bring about alteration in the humus substrate, which may in turn react on the behaviour of new plantings if made during a period of ecological instability. Also, when attempting experimentally to introduce suitable mycorrhiza-formers in a soil inoculum from a native stand of the species concerned, there is a danger of bringing in also undesirable soil fungi—relatively innocuous under native conditions, but very deleterious to growth when introduced into a new soil environment. There is good reason, also, to suspect that the poor growth shown by some so-called geographical races of, say, Scots pine or Sitka spruce, may be directly associated with—among other factors—maladjustment in respect to the species or strains of mycorrhizal fungi available.

In general, it may be safely concluded that the mycorrhizal relations of trees in natural soils are with native fungi growing freely in these soils, and that these must therefore be included as ecological factors of great or even critical importance in any ecological concept of the habitat.

Dr A. Foggie. I should like to make a few very brief remarks on some instances bearing on this problem which I have noticed in Cyprus and West Africa. These remarks are merely observations, there are little or no detailed records or research to back them, for if we know little enough of fundamental causes in this country, in the colonies we know considerably less.

First in Cyprus. In the hill forest area in which I spent most of my time, the principal timber species was the pine, *P. halepensis*, which must undoubtedly be classed as a pioneer species, exceedingly drought resistant and when established capable of growing successfully on the bare deeply fissured andesitic rocks which constitute the soil, so called, over large parts of the area. When mature and its bark had not been destroyed by blazing for resin tapping it was also resistant to fire and there was evidence that it had replaced the cedar, *Cedrus brevifolia*, over large areas of the Paphos Forest, the cedar only occurring in four small isolated relics to which it had been reduced by fire and goat grazing to the advantage of the pine. There was also evidence that the Aleppo pine had occupied areas formerly stocked by the Troodos pine, *P. nigra* var. *Pallasiana* or *Caramannica*, after the heavy fellings of 1914–19 in Troodos Forest. Some of the best areas of young crops were also to be seen on abandoned vineyards from the rapid colonization of bare cultivated soil. In these cases there was a soil of about 18 in. depth, a red-brown light sandy loam.

In the forest area which I knew best, there was little artificial regeneration or afforestation as the major part of the crop was being worked under a group selection system, but owing to fires we had a certain amount to do. This was attempted by sowing or planting one-year seedlings of Aleppo pine on lines along the contours. I say attempted as the success in early years was negligible. In this country a forester is troubled if he only attains an 80% or so successful establishment three or four years after planting. In Cyprus, if we had about 20% survival after the first summer and 10% after the second we thought there might be some chance of success and the method was worth continuing. Only sowing, or planting one-year seedlings, gave these partial successes. Using larger plants, two-year seedlings, one-year transplants or more, you were almost certain of a 99·9% failure except in gully bottoms or by springs, as the root systems were quite unadapted to secure the necessary moisture in the planting area. And this was using an indigenous hardy pioneer species, seed being of strictly local origin, and of which there might be flourishing crops all round the burned area whose reafforestation was being attempted.

The Aleppo pine was mycorrhizal in rooting, flourishing seedlings in the nursery having fine mycorrhizal club rootlets; and influenced by reading of Dr Rayner's early work at Wareham, I thought the mycorrhizal fungi might have been destroyed in the surface soil by the fire. Experiments proved this was not the major cause if it occurred at all and it was left to Mr Chapman, my successor in the Division, to show that the major causes of death were heat lesions and sun scorch, the surface temperature of the soil either reaching the critical temperature of over 120° F. and causing heat lesions, or the air round the aerial shoot, owing to radiation from rock faces or lack of local circulation, reaching the same temperature.

The pine, though undoubtedly a pioneer timber tree species, is not under these conditions a member of the primary sere. Untouched, a burned area in the Cyprus pine forests is colonized after the winter rains by a flush of annual or short-lived grasses and a flush of new shoots from the roots of the *Cistus* and other subshrubs forming the regular forest floor, and it is only after these have grown up to give partial shelter to the pine seedlings that successful regeneration by the pine occurs. It must be remembered that the Mediterranean vegetation except in definitely wet spots is not a closed vegetation; there is always bare ground between the individual plants where new-comers can start and survive if they can compete with the occupants for water, and here the seedling of the pine which will send a tap-root of over 6 ft. length down after moisture in its first growing season is well equipped to compete with the shrubs. A *Cistus* cover is not at all like dense heather cover.

That this was what did occur in nature could be seen in a burned area dating from 1924 in which attempts at artificial restocking about 1928 had entirely failed and had been abandoned as the area could not be adequately protected from goat grazing, but when I last saw it in 1936 large areas where the *Cistus* was fairly luxuriant were filling up with pine regeneration browsed to the level of the *Cistus* by the goats.

In many cases, however, we could not leave areas to recover slowly by this method, the erosion was too great. The average slope in Paphos was 30°. In such cases we had artificially to stabilize the soil by brush and stone terraces, cut contour trenches, sow them up with pine and artificially create the conditions necessary to success by setting up brushwood shades above them. Laying brushwood over the soil merely created conditions for sun scorch by preventing air circulation round the seedlings.

Therefore the forester must not confine himself merely to the succession of the woody species he is interested in, he must know the dynamic ecology of the whole biome (cf. hawthorn and beech on Buriton).

West Africa provides entirely different conditions. There the problem is not to get things to grow but to prevent too many growing. The species which present conditions of demand render commercially valuable, and which the forester therefore wishes to grow in greater quantity, are a mere dozen or so out of about 200 species occurring in the upper canopy of the natural forest with 1000 or more woody species.

Those I worked with were the mahoganies, *Khaya ivorensis*, *Entandrophragma* spp. as species of primary importance and *Triplochiton scleroxylon*, *Terminalia ivorensis* and *Guarea* spp., as species of secondary importance. Of these species, those of primary importance occur in what is considered the climax forest, but sparingly. *Khaya* and *Entandrophragma* though present in all types only occur as characteristic dominants in an area where rainfall and soil give a slightly less moist environment described by Chipp as a preclimax. *Chlorophora excelsa* occurs in the climax association and in all preclimaxes, but, from its size-class distribution there, does not appear to be maintaining itself in any of them. It appears to require conditions of a sere or subsere to establish itself when its apparent longevity allows it to hang on into the climax or preclimax stage. I say apparent longevity as all ecological work in the tropics is greatly hindered, as few of the trees have visible growth rings and for those that have, it has not been determined what relationship they bear to the seasons or chronological year.

The artificial regeneration practised in the Gold Coast is all by 'taungya' methods, the forest being felled and burned, then the soil between the stumps cultivated by the native farmers by hoeing, and a new tree crop and their agricultural crops, corn and plantains, being put in simultaneously. Stumped plants are used. The area is farmed three years then the regrowth of coppice and seral weeds, herbaceous climbers, shrubs, e.g. *Alchornea*, and the short-lived weed trees *Musanga Smithii* and *Trema* sp. is so great that the return to be expected from further cultivation is not worth the work and the farm is abandoned. Present forestry practice is, however, to continue clearing along the lines of planted trees, which are fairly widely spaced, and do not and will not form a canopy for a considerable time as the *Khaya*, *Entandrophragma* and *Chlorophora* do not form a wide crown in early youth but simply send one strong leader upwards. In this we do not know whether we are following Sir Roy Robinson's silvicultural stream or not. From nursery work and early planting experience we know that the *Khaya* and *Entandrophragmas* like a lot of light and *Chlorophora* a fair amount of light for rapid growth. *Khaya* planted in narrow lines in the original forest without disturbance of the upper canopy simply stood still or died. Yet in untouched forest occasional seedlings can be seen and often a fair proportion of small trees reaching the upper canopy occur as well as the big mature dominants, especially in the *Khaya-Entandrophragma* preclimax. Work of this nature with indigenous species is very much in its infancy in the Gold Coast and we do not yet know what success will attend these plantations in later life, but it might be preferable to let the weed tree species, *Musanga* and *Trema*, form a canopy and let the *Khaya* and *Entandrophragma* push their way through, when these short-lived species collapse. They would then, however, have to compete with *Ricinodendron africanus* and many other rather longer-lived trees which also appear in abundance. Among them are *Triplochiton scleroxylon* and *Terminalia* spp., principally *T. ivorensis* in the Gold Coast, which are species having a commercial value at present.

In Nigeria, a method is being tried, which was just being started in the Gold Coast when I left, of planting alternate lines with *Triplochiton* and *Terminalia* as these species develop comparatively broad crowns in youth, to see if they would form canopy between the mahogany rows and suppress the *Musanga*, *Trema* and other weed species, then grow up with the mahoganies, thus cutting out ('telescoping') one state in the probable succession.

Until a proper knowledge is obtained of successional phases within the natural forest and in man-made seres, however, our silvicultural practices will be purely empirical of the hit and miss variety.

Professor T. G. B. Osborn. Professor Osborn accorded warmest welcome to the offers of co-operation between forester and ecologist made by Sir Roy Robinson. This was a very productive field, and he hoped that both ecologist and forester would derive great benefit from future collaboration. There had been expressed certain criticisms of the concept of the silvicultural stream, for the most part on the grounds that it oversimplifies what is in fact a very complex phenomenon. Sir Roy was, however, familiar with many streams, and he undoubtedly, in putting forward his hypothesis, had in mind the 'braided' stream, with its many channels and currents. He wished to emphasize Professor Champion's reference to the great diversity of forest conditions in our small islands. Differences of rainfall alone would account for much of this, not to mention variations in soil, aspect, geological strata and the like. He would also support Professor Steven in his references to the necessity of determining whether or no a community represents an edaphic climax before planning an afforestation programme.

Dr E. W. Jones. Dr Jones vied with Dr Blackman in expression of the humbleness of the ecologist before the enquiring forester. Ecological work may be of two main kinds, (*a*) that devoted to the elaboration and study of ecological theories and concepts, and (*b*) the close study of environmental conditions and their effects on the individual, including here, autecological work. On the basis of theory and concept the forester often asks what is the course of succession and the nature of the climax. The ecologist's evidence is, however, very tenuous. There is very little concrete evidence as to the nature of the climax in the North Temperate Zone, and our views on it are highly theoretical. In North America 90% of this climax was destroyed before it could be examined, and this particularly in the east, where it most resembles the European. The idea also of selective regeneration may be called into question. The course of events is too often cataclysmic. A stand matures, and then falls to pieces and is replaced by another which may not necessarily be of the same species.

But in autecology we are on safer ground, and can be of much greater immediate use, provided that the ecologist becomes more familiar with the problems confronting the applied scientist, be he forester or agriculturalist. The practical man, however, already knows much of what the ecologist is still groping after.

Dr A. R. Clapham. Dr Clapham referred to the opposition of interests already mentioned by Dr Stamp, between agriculturalist and forester, in that both are after the same land, the one for grassland improvement on hill grazings, the other for afforestation. He asked also for the preservation of at least some fragments of our old broad-leaved woodlands for ecological study, pointing out that it was from the examination of these that much information could be derived which would aid the forester in planning his future programmes.

Referring to the Biological Flora, now in course of preparation by the Society, he indicated the importance of the autecological studies which it comprised. He suggested that this flora was not confined to our native species, and it would be invaluable if members of the guest societies would offer memoirs on exotic trees, such as the larch, Norway spruce and the like.

Mr W. R. Day. *Exposition and research.* There is need not only for ecological research into problems concerned with forestry but also for the exposition and demonstration of ecological principles and ideas in the simplest and clearest possible manner. Foresters, especially when discussing silvicultural matters, inevitably enter the sphere of ecology, silviculture being largely applied ecology. It is of the greatest importance that thought shall be clear and accurate on such matters; but this is not possible unless those whose duty it is to develop the fundamental science express themselves in a manner which is clear and understandable to those who apply it.

Reconnaissance surveys. Ecological reconnaissances are probably of particular importance in Forestry at the present time. In forest administration it is necessary to make decisions within a short time; the results of long-term research cannot be waited for. Such decisions, made before the ultimate results of long-term research are available, need to be based on adequate working hypotheses if unduly large errors are to be avoided. Reconnaissance has the function of discovering the nature of the problems awaiting solution and with which administrative activity is concerned, and of formulating working hypotheses as to their probable fundamental explanation. In this way relatively well informed and certain action can be taken while the results of long-term research are awaited.

It is plain, also, that if any survey of the potential suitability of land for agriculture or forestry is to be made, as suggested by Dr Dudley Stamp, it must be begun as a reconnaissance, for a detailed survey of the whole of Britain would take too long when the purpose of the survey which is of first importance is to provide data for administrative action in the immediate future. The need for the carrying out of such a reconnaissance survey in accordance with statistical principles, the need for which in ecology was stressed by Dr Blackman, must be obvious.

Autecological studies. A number of speakers stressed the need for these. This need becomes very plain if the pathology of any species of tree is considered as a whole. It is not possible to understand the causes of health and disease in the case of any particular species, without understanding or at least attempting to obtain a conception of the autecology of the species concerned. For health or disease is the result of the interaction of factors of the environment on an organism of a particular constitution. Ultimately this constitution and the physical and biotic factors concerned must be understood if a perfect realization of the laws determining health and disease is to be obtained. An autecological study should thus aim at presenting a view of the whole of the physical and biotic relationships of a species.

The concept of fertility might well be developed in connexion with autecology. A particular strain of any species will obtain its optimum development in a particular physical environment and in association with particular plants and animals. Any departure from the optimum will involve corresponding variations in the environment. One is defining the fertility of the sites concerned in defining growth after this manner. This is, I feel, a matter of considerable importance to foresters whose great difficulty very often is to see the wood for the trees.

Soil studies. A number of speakers expressed the importance of soil studies in ecology. As a pathologist I feel there is need to stress this at the present time. The environment of the root of trees, and the growth of roots in relation to this, is inadequately understood. The mycorrhizal studies of Dr Rayner, the various forms of deficiency disease; the difficult and complex problems involved in the root diseases of the larger trees, have only to be mentioned in order to realize this. These are all involved in the problem of fertility, mentioned above, if any fundamental view of the matter is taken. The need for understanding the range of variation in soil conditions is also to be stressed.

Dr A. J. Wilmott. A. J. Wilmott, speaking as a systematic botanist, stressed Dr Clapham's plea for the preservation of a sufficient amount of our natural vegetation. The laboratory of the systematist was, he said, natural vegetation in which the distributions of species and forms could be studied, for data of distribution were his fundamental facts. The interference resulting from all this planning, planting and other economic activities, was as if someone went into a chemist's laboratory and started throwing the bottles about and smashing them. He hoped that some of the real ancient woodlands—and as a systematist he could say from the species in the woods which were real old woods—would be spared. He agreed with Professor Osborn that in this country there were different edaphic climaxes; he could not understand how any field botanist could treat all our woodlands as parts of a single climatic climax. As an example of avoidable failure in planting he referred to his observation in Yorkshire of a dale bearing fine old beech wood on one side of a valley and a cleared slope on the opposite side planted with small conifers—all soon dead. He thought that any ecologist might have been able to foretell that result, but who was responsible he did not know. He referred to the presence of woodland species on the lower rock ledges of Beinn Laoigh, and forest timber in the neighbouring bogs, as in so many parts of Scotland, even on cols high up, which suggested that timber could be grown in quantity to-day in Scotland, although possibly these woodlands might belong to a period of different climate and their absence to-day be due not merely to the prevention of regeneration by browsing deer. (The main thing, from the systematist's point of view, was that the data concerning exactly what has been planted, and where and whence, should be preserved in an available form, so that the discovery of fresh species in any area could be interpreted with some degree of probability or certainty, as being perhaps a rare overlooked species favoured by the changed conditions, or as a definitely introduced plant, brought in with such and such a species from such and such a place in which it was known to occur. These data should be preserved even if their usefulness to the forester had passed, and would gladly be kept at the Natural History Museum.)

The Chairman, in calling upon Sir Roy Robinson to reply to the important issues raised during the meeting, remarked on the unfortunate lack of reference to the role of the smaller animals in preserving the conditions of woodland habitats. Quite apart from the woodland pests, on which many adequate studies have been published, the general invertebrate fauna comprises important sections of forest communities, of which we have all too little knowledge. It is to be hoped that this gap will ultimately be filled, to the mutual benefit of foresters and ecologists.

Sir Roy Robinson (summing up). I have listened with care to the whole of this discussion. It is scarcely possible for me to cover it all in the time that remains and therefore I will confine my remarks to two or three points.

In the first place I do not assess my two working hypotheses as 'rules' to which foresters should adhere but merely as lines of thought which in the event may or may not turn out to be correct but in any event can serve to focus attention on what are undoubtedly important issues.

Then I do not want to infer with regard to the silvicultural stream that it is desirable in every case, or even in most cases, to go the whole course. As Professor Champion points out it may be necessary to remain anchored or occasionally to work up-stream. What I do think, however, is that in both cases explanations of some of the difficulties which then arise may be sought in the theory of Ecological Successions.

I agree as to the necessity for laying down ecological reserves. The Forestry Commission in association with ecologists have already made a beginning and are prepared to go further. To get the full value out of reserves it will be necessary to undertake and periodically repeat a great deal of descriptive work. The Commission can and will afford the facilities but foresters have not the time to spare from routine duties nor the specialized training. I trust therefore that the Society will formulate its ideas in some detail so that the venture may go forward smoothly. I hope, too, that the problems will be regarded, as our Chairman has pointed out, as not only botanical but also as biological in the widest sense of the term.

REFERENCES IN THE BIOLOGICAL FLORA

At the present stage in the development of the Biological Flora the necessity for a settled policy in the matter of references has become clear. It is obvious that the flora would lose much of its value if the sources of information other than the authors' own observations are not clearly indicated. On the other hand, the accounts will become unreadable if they are overloaded with too large a number of references. In order to steer a middle course the following recommendations are put forward. It should be borne in mind that they are not more than recommendations and need not be adhered to when there is a good reason for doing otherwise.

(1) As has already been the practice, unpublished information received verbally or in correspondence should be referred to by the name of the informant, without date, in brackets.

(2) In general, references should be given for all information taken from other publications, bearing in mind that the object of such references is either (*a*) to direct the reader to fuller information on a particular subject, or (*b*) to indicate the authority for a definite statement of fact and so help the reader to form his own judgement about its reliability, as well as to make revision possible in the light of later work. References may be omitted for facts which are generally known or are quoted in most of the readily available standard works. Thus they need not be given for the established geographical range of a species, but should be given for recent additions to its range and for its altitudinal distribution, British and foreign.

(3) A list is given below of certain standard works which are likely to be referred to very frequently in the flora. These should be referred to in the text by the abbreviations indicated and should not be listed in the bibliography.

(4) With the exception of the works considered under (3), references should be given in the standard form used in the *Journal*, viz. (Tansley, 1911). A page reference may be added where the reference might be difficult to trace, either because the paper is long or because the information occurs incidentally in a paper mainly on a subject other than that under consideration.

(5) In the bibliography the references should appear with title according to the usual form, viz.

For books: **Willis, J. C. (1920).** *Age and Area.* London.

For papers: **Watson, W. (1932).** The bryophytes and lichens of moorland. *J. Ecol.* **20**, 284–313.

If desired books and papers not quoted in the text may be included in the bibliography.

WORKS TO BE REFERRED TO IN THE 'BIOLOGICAL FLORA' BY STANDARD ABBREVIATIONS.

(*a*) *Botanical*

Ascherson, P. & Graebner, P. (1896–). *Synopsis der mitteleuropäischen Flora.* 8 vols. Leipzig.	Refer to vols. as Aschers. & Graebn. **1**, etc. (incomplete).
Colgan, N. & Scully, R. W. (1898). *Cybele Hibernica.* Dublin.	Cyb. Hib.
Druce, G. C. (1932). *The Comital Flora of the British Isles.* Arbroath.	Comit. Fl.
Hegi, G. (1908–31). *Illustrierte Flora von Mitteleuropa.* 7 vols. München.	Refer to vols. as Hegi Fl. **1**, etc.
Kirchner, O., Loew, E. & Schroeter, C. (1908–). *Lebensgeschichte der Blütenpflanzen Mitteleuropas.* 1 vol. (incomplete).	Refer to vols. as Lebensg. **1**, etc.

Maude, P. F. (1939). The Merton Catalogue. *New Phytol.* **38**, 1–31.	Mert. Cat.
Praeger, R. Ll. (1901). *Irish Topographical Botany.* Dublin.	Ir. Top. Bot.
Praeger, R. Ll. (1934). *The Botanist in Ireland.* Dublin.	Bot. Irl.
Ridley, H. N. (1930). *Dispersal of plants throughout the world.* Ashford.	Ridley, Disp. plts.
Rouy, G. & Foucaud, J. (1893–1913). *Flore de France.* 14 vols. Asnières, Rochefort and Paris.	Refer to vols. as Rouy Fl. **1**, etc.
Salisbury, E. J. (1942). *The Reproductive Capacity of Plants.* London.	Salisb. Rep. Capac.
Schroeter, C. (1926). *Das Pflanzenleben der Alpen*, 2nd ed. Zürich.	Schroeter, Pflanzenleben.
Tansley, A. G. (1939). *The British Isles and their Vegetation.* Cambridge.	Tansley, Br. Isl.
Watson, H. C. (1847–59). *Cybele Britannica.* 4 vols. London.	Refer to vols. as Cyb. Brit. **1**, etc.
Watson, H. C. (1883). *Topographical Botany*, 2nd ed. London. Supplements in *J. Bot., Lond.*, **43**, 1905 (by A. Bennett) and *J. Bot., Lond.*, **58**, 1930 (by A. Bennett, C. E. Salmon & J. R. Matthews).	Top. Bot. and Top. Bot. Suppl. 1 & 2.
Wilson, A. (1929–31). Altitudinal range of British plants. Supplement to *Northw. Nat.*, **6**, and **7**.	Alt. range Br. Pl.

(*b*) *Mycological*

Bisby, G. R. & Mason, E. W. (1940). List of Pyrenomycetes recorded for Britain. *Trans. Brit. Myc. Soc.* **24**, 127–243.	List Pyrenomyc.
Grove, W. B. (1913). *The British Rust Fungi.* Cambridge.	Br. Rust F.
Grove, W. B. (1935, 1937). *The British Stem and Leaf Fungi* (*Coelomycetes*). 2 vols. Cambridge.	Refer to vols. as Br. Stem and Leaf F. **1** and **2**.
Oudemans, C. A. J. A. (1919). *Enumeratio Systematica Fungorum.* 5 vols. The Hague.	Refer to vols. as Oudemans, Enum. **1**, etc.
Phillips, W. (1893). *A Manual of the British Discomycetes.* London.	Man. Br. Discomyc.
Rea, C. (1922). *The British Basidiomycetes.* Cambridge.	Rea, Br. Basidiomyc.
Saccardo, P. A. (1884–1931). *Sylloge Fungorum.* 25 vols. Padua.	Sacc. Syll.
Sampson, K. (1940). List of British Ustilaginales. *Trans. Brit. Myc. Soc.* **24**, 294–311.	List Ustilag.
Wakefield, E. M. & Bisby, G. R. (1941). List of Hyphomycetes recorded for Britain. *Trans. Brit. Myc. Soc.* **25**, 49–126.	List Hyphomyc.

(*c*) *Entomological, etc.*

Butler, E. A. (1923). *A biology of the British Hemiptera-Heteroptera.* London.	Butler, Hem.-Het.
Edwards, J. (1896). *The Hemiptera-Homoptera of the British Islands.* London.	Edwards, Hem.-Hom.
Fowler, W. W. (1887–1913.) *The Coleoptera of the British Islands.* 6 vols. London.	Refer to vols. as Fowler, Coleopt. **1**, etc.
Goodey, T. (1940). *The Nematode Parasites of Plants Catalogued under their Hosts.* Imperial Bureau of Agricultural Parasitology (Helminthology), St Albans.	Nemat. Cat.
Hendel, F. (1931–6). *Agromyzidae* in Lindner's *Die Fliegen der Paläarktischen Region*, **59**, Lief. 52, 54, 56, 58, 66, 85, 90, 92, 94, 96. Stuttgart.	Refer to Lieferungen as Hendel, Lief. 52, etc.
Houard, C. (1908–13). *Les Zoocécidies des plantes d'Europe et du Bassin de la Mediterranée.* 3 vols. Paris.	Refer to vols. as Houard, **1**, etc.
Kunth, P. (1906–9). *Handbook of Flower Pollination.* Trans. J. R. Ainsworth Davis. 3 vols. Oxford.	Refer to vols. as Kunth, Poll. **1**, etc.
Meyrick, E. (1928). *A Revised Handbook of British Lepidoptera.* London.	Meyrick, Lepidopt.
Theobald, F. V. (1926–9). *The Plant Lice or Aphididae of Great Britain.* 3 vols. London.	Refer to vols. as Theobald, Aphid. **1**, etc.

BIOLOGICAL FLORA OF THE BRITISH ISLES

ACCOUNTS PUBLISHED OR IN PREPARATION

The accounts already published are:

Juncus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. inflexus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. effusus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. conglomeratus L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
J. subnodulosus Schrank, by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
Zostera L., by T. G. Tutin. *J. Ecol.* **30**, no. 1.
Z. marina L., by T. G. Tutin. *J. Ecol.* **30**, no. 1.
Z. hornemanniana Tutin, by T. G. Tutin. *J. Ecol.* **30**, no. 1.
Cladium mariscus R.Br., by V. M. Conway. *J. Ecol.* **30**, no. 1.
Aster tripolium L., by A. R. Clapham, W. H. Pearsall and P. W. Richards. *J. Ecol.* **30**, no. 2.
Juncus filiformis L., by P. W. Richards. *J. Ecol.* **31**, no. 1.
Juncus macer Gray, by P. W. Richards. *J. Ecol.*, **31**, no. 1.
Rhamnus cathartica L., by H. Godwin. *J. Ecol.* **31**, no. 1.
Frangula alnus Mill., by H. Godwin. *J. Ecol.* **31**, no. 1.
Tamus communis L., by I. H. Burkill. *J. Ecol.* **32**, no. 1.

These may be obtained from the Cambridge University Press, 200 Euston Road, N.W. 1, at 1*s.* each. Standing orders for all parts issued may be placed at the reduced price of 9*d.* each.

The following are being prepared:

Acer campestre L. and *A. pseudo-platanus* L., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.
Aconitum anglicum Stapf, H. A. Hyde, National Museum of Wales, Cardiff.
Adoxa moschatellina L., Prof. M. Skene, The University, Bristol.
Allium ursinum L., T. G. Tutin, c/o The Botany School, Cambridge.
Allium vineale L., Miss R. H. Scott, c/o The Botany School, Cambridge.
Andromeda polifolia L., Prof. W. H. Pearsall, F.R.S., Department of Botany, The University, Sheffield.
Arenaria verna L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.
Arenaria norvegica Gunn., Dr W. A. Clark, King's College, Newcastle-on-Tyne.
Asperula odorata L., Dr A. R. Clapham, Department of Botany, Oxford.
Blackstonia perfoliata (L.) Huds., Dr B. Colson, University Department of Botany, Reading.
Carlina vulgaris L., *Cirsium palustre* (L.) Scop. and *C. vulgare* (Savi) Airy-Shaw (=*C. lanceolatum* (L.) Scop.), Dr W. A. Sledge, University Department of Botany, Leeds 2.
Corallorrhiza trifida Châtel., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.
Daphne laureola L., Dr P. W. Richards, The Botany School, Cambridge.
Elymus arenarius L., T. E. T. Bond, Tea Research Institute, Ceylon.
Eriocaulon septangulare With., Dr Leighton Hare, Jodrell Laboratory, Royal Botanic Gardens, Kew.

Galium erectum Huds. and *G. mollugo* L., Miss M. Priestley, c/o The Botany School, Cambridge.
Glyceria maxima (Hartm.) Holmb., Miss J. M. Lambert, Westfield College, Oxford.
Goodyera repens R.Br., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.
Helictotrichon (*Avena*) *pratense* (L.) Pilger and *H. pubescens* (Huds.) Pilger, Dr G. Carson, School of Agriculture, Cambridge.
Juncus articulatus L., em. Wahlenb. and *J. acutiflorus* Ehrh. ex Hoffm., Dr A. R. Clapham, Department of Botany, Oxford.
Juncus squarrosus L., Prof. W. H. Pearsall, F.R.S., University Department of Botany, Sheffield.
Juncus triglumis L., Dr W. A. Clark, King's College, Newcastle-on-Tyne.
Juniperus communis L., T. G. Tutin, c/o The Botany School, Cambridge.
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Leucojum aestivum L., Dr F. B. Hora, University Department of Botany, Reading.
Limosella aquatica L., Dr F. W. Jane and Miss R. Dowling, Department of Botany, University College, Gower St, London, W.C. 1.
Limosella subulata Ives, Dr K. Blackburn, King's College, Newcastle-on-Tyne.
Listera cordata (L.) R.Br., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.
Lloydia serotina (L.) Reichb. and *Lobelia dortmanna* L., Dr N. Woodhead, University Department of Botany, Bangor, North Wales.
Luzula forsteri (Sm.) DC. and *L. pilosa* (L.) Willd., Prof. T. Harris, University Department of Botany, Reading.
Melandrium dioicum (L.) Coss. & Germ. and *M. album* (Mill.) Garcke, H. G. Baker, Hosa Research Laboratories, Windmill Road, Sunbury-on-Thames, Middlesex.
Myosotis arvensis (L.) Hill, *M. collina* Hoffm. and *M. versicolor* Sm., A. E. Wade, National Museum of Wales, Cardiff.
Naias flexilis Rostkov, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
Nardus stricta L., R. Elfyn Hughes, Department of Agricultural Botany, Bangor.
Narthecium ossifragum (L.) Huds., Dr Mollison, University Department of Botany, Old Aberdeen.
Ophrys arachnites Hoffm., Francis Rose, The Forge House, East Malling, Kent.
Orchis fuchsii Druce, *O. elodes* Gris., *O. latifolia* L. sec. Pugsl. (*O. incarnata* auct. angl.) and *O. purpurella* Stephenson, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
Orchis purpurea Huds., Francis Rose, The Forge House, East Malling, Kent.
Polygonum persicaria L., etc., N. Simmonds, c/o The Botany School, Cambridge.
Potamogeton coloratus Hornem., *P. filiformis* Pers. and *P. pectinatus* L., Prof. J. W Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
Potamogeton gramineus L. and *P. rutilus* Wolfg., Dr W. A. Clark, King's College, Newcastle-on-Tyne.
Quercus robur L. and *Q. petraea* (Mattuschka) Liebl., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.
Rhynchospora alba (L.) Vahl and *R. fusca* (L.) Ait. f., Miss E. Canton, Department of Biology, Technical College, Sunderland.
Rosa spp. (excl. *R. arvensis, micrantha* and *tomentosa*), Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
Rumex spp., J. E. Lousley, 7 Penistone Road, Streatham Common, S.W. 16.
Scilla non-scripta (L.) Hoffmanns. & Link, Dr G. E. Blackman, Imperial College of Science, London, S.W. 7.

Sedum acre L., Dr B. Barnes, Department of Biology, Chelsea Polytechnic, London, S.W. 3.

Sonchus asper (L.) Hill and *S. oleraceus* L., emend. Hill, R. A. Lewin, c/o The Botany School, Cambridge.

Sonchus palustris L., Francis Rose, The Forge House, East Malling, Kent.

Spiranthes stricta Nels., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Stellaria nemorum L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Subularia aquatica L., Dr N. Woodhead, Department of Botany, Bangor.

Thlaspi alpestre L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Tilia cordata Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.

Trientalis europaeus L., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Ulmus spp., Dr R. Melville, The Herbarium, Royal Botanic Gardens, Kew.

Urtica spp., P. Greig-Smith, c/o The Botany School, Cambridge.

Valeriana officinalis L. and *V. sambucifolia* Mikan, J. Carpenter, c/o The Botany School, Cambridge.

Viburnum lantana L. and *V. opulus* L., Dr H. Godwin, The Botany School, Cambridge.

Viola lutea Huds. and *V. tricolor* L., Dr P. E. Fothergill, King's College, Newcastle-on-Tyne.

Wahlenbergia hederacea Reichb., Francis Rose, The Forge House, East Malling, Kent.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account singly or in collaboration should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

Accounts ready for publication should be sent to Dr P. W. Richards, Botany School, Cambridge.

BIOLOGICAL FLORA OF THE BRITISH ISLES

L.C. (Ed. 11) No. **1849**

TAMUS L.

One British species.

Tamus communis L.

I. H. Burkill

A tall herb, twining to the left, springing from a dark-coloured perennial tuber of variable shape. Stems unbranched, 2–4 m. long. Leaves alternate, cordiform, with deeply cordate base, commonly with a light lateral constriction, entire, finely acuminate, 3–10 × 2·5–10 cm., dark green and glossy, net-veined with 3–9 main ribs diverging from the base; petiole on a pediment of stem tissue bearing 2 stipule-like emergences (the equivalent of the prickles in *Dioscorea*). Dioecious; flowers yellowish green in axillary racemes, the female shorter and fewer-flowered than the male. Perianth of the male flowers campanulate, 3 of the lobes overlapping the others, those of the female flowers free. Stamens 6, sometimes represented in the female flowers by minute staminodes. Style columnar, divided above into three bilobed recurved stigmas. Berry globose, red when ripe, containing 1–6 spherical seeds.

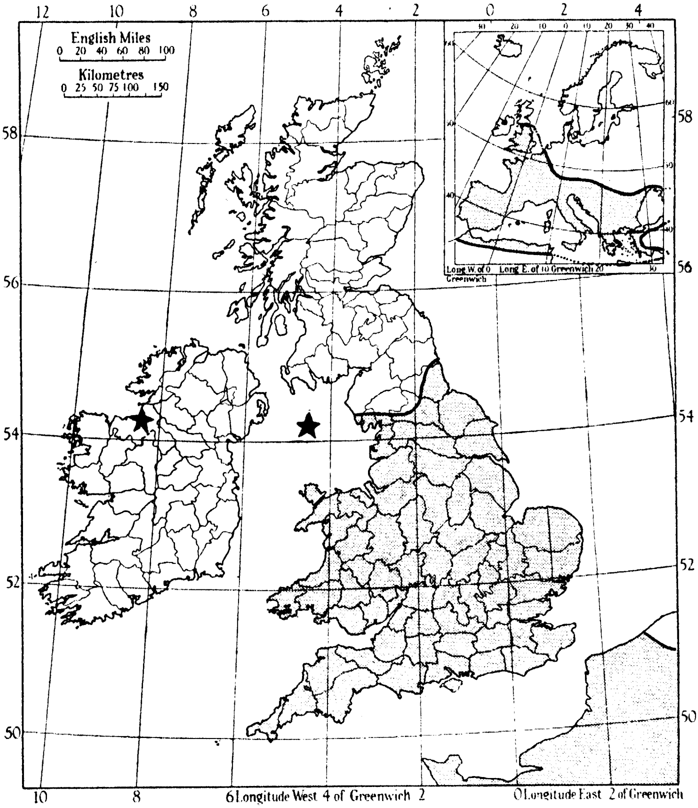

Fig. 1. *Tamus communis* L.: vice-comital distribution in the British Isles, and (inset) distribution in Europe.

Has no named varieties in Britain, though there is variation in the shape of the leaf and a variety with ellipsoidal berries occurs. A variety with yellow berries (var. *smilacifolia* Rouy & Fouc.) has been found in France.

A mesophyte of wood margins, scrub and hedges, avoiding dry climates and very wet or very dry soils.

I. *Geographical and altitudinal distribution.* In all the vice-counties of England as far north as the southern edge of the Cumbrian mountains (54° 20′ N.) in the west and the neighbourhood of Newcastle-on-Tyne (55° N.) in the east. In the Isle of Man (71) only a solitary plant has been found, doubtless an accidental introduction. In Ireland only about Lough Gill in Sligo (28) and Leitrim (29). First recorded in Ireland in 1866 and believed by More (1873, p. 145) to be planted, but accepted by Praeger (Bot. Irl. para. 420) as native: the present writer is convinced that it was introduced, accidentally or intentionally, in the last century.

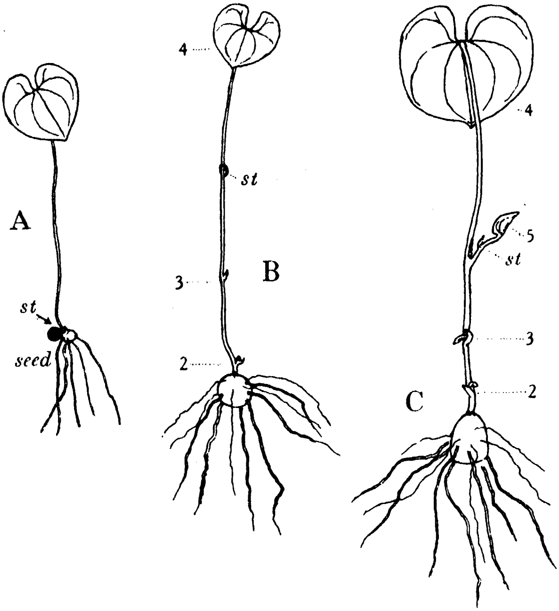

Fig. 2. *A*, seedling of the first year, showing the single assimilating leaf on a long petiole, the seed, the tuber of the same size as the seed, and the downwardly directed roots. *B*, seedling of the second year, the stem with three internodes developed, the single leaf appearing terminal, having pushed the end of the stem aside. *C*, a seedling of the third year, in which the larger assimilating leaf has not completely suppressed the stem, but the little-developed leaf following it has. The calyptrate scale leaf at the base of the stem cannot be seen, the other foliar organs are numbered. *st* indicates the position of the apex of the stem. The growth of the tuber is indicated and the reduction of the older roots to a wiry state by decortication. All × $\frac{1}{2}$.

Widely distributed from the British Isles, Belgium and Morocco in the west, through south-eastern Europe and the Mediterranean to the Caucasus and the southern border of the Caspian. The north-eastern boundary runs as a continuous line through Mainz, along the Rhine to Constance, and thence near 47° N. through Austria and Hungary to Transylvania and the northern shore of the Black Sea. The southern boundary runs along the Great Atlas to Tunis; there is an outlier in Cyrenaica and it reappears in northern Palestine and Syria, then skirts the highlands of Asia Minor close to the Aegean and Black Seas. Drought is probably the limiting factor southwards and cold towards the north-east.

A lowland species in England, ascending to 180 m. near its northern limit and to 250 m. in the southern Pennines and the Peak of Derbyshire. In the Alps to 1100 m. in Valais (Jaccard, quoted in Aschers. & Graebn. **3**, 438) and to 1300 m. in southern Tirol (Sarnthein, ibid.). To 1300 m. in the Great Atlas of Morocco (Braun-Blanquet & Maire, 1924, p. 175).

Likes the neighbourhood of mountains and sea coasts, owing to the high rainfall, also that of large lakes (e.g. Lake Balaton in Hungary and the larger lakes of Switzerland and northern Italy) owing to the locally high atmospheric humidity, but in certain parts of Switzerland it avoids the wetter faces of woods apparently owing to the excessive humidity (Lebensg. **1**, 936). To the south of the Black Sea on the approaches to the dry steppes of Asia Minor it grows in valleys running east to west which do not serve as channels for dry *föhn* winds (Radde, 1901, p. 36).

II. *Habitat.* Requires a moist, friable, well-drained soil. The chemical properties of the soil appear to matter to it less than the physical, though it does appear to demand basic or at least neutral conditions; thus in beechwoods it is absent in the acid 'Heath' beechwoods, and in those of the non-calcareous chalk plateau, except Watt's 'Type (*a*)', which is transitional to the calcareous types (Watt & Tansley, 1932, p. 324). It avoids chalk only if the soil over it is too dry. The places where it grows are always well supplied with leaf mould from the associated woody plants.

In the relatively continental climate of Cambridgeshire it tends to avoid both the excessively dry soils on the borders of Breckland and the insufficiently drained soils of the fens. For the same reason as it avoids the fens it does not border streams. In east Norfolk, however, it occurs in both fen carr and swamp carr, but not in abundance except sometimes on the edges (E. A. Ellis). Its sensitiveness to the water content of the soil leads to an interesting contrast between its distribution on the North and South Downs; it is absent from the latter, except at the western end, but on the former, owing to the prevalence of moisture-retaining loams overlying the chalk, it is very common. It is evidently near its limits of tolerance on the North Downs, as it tends to be plentiful on the damper rather than on the drier side of a hedge and on the eastern and northern edges of a wood rather than on the sunnier western and southern edges. Chalk is more inimical in the Mediterranean region than in more northern climates.

It normally grows in the shade of trees or shrubs. Beck (1901, p. 158 and cf. p. 153) records it as characteristic of the rocky heaths of Dalmatia, where, though shrubs are present, shade is provided mainly by rocks. On sea cliffs in south-west England it occasionally grows in the shelter of rocks without a cover of shrubs. Solitary shrubs do not provide enough shelter, a thicket or hedgerow being needed. Hedges periodically trimmed provide ideal conditions and are its commonest habitat from Britain to the Balkans (cf. Adamovic, 1909, p. 297). Hawthorn, if not cut back, may suppress it by excessive shading; similarly, different species of trees suppress it according to the shade cast. It may, however, persist in shade without flowering for a number of years. Among bushes on the edge of the shade of a tree it finds a narrow belt in which conditions of light and humidity are favourable; seed falling farther out finds conditions too dry to germinate, seedlings farther in undergo suppression.

Into the shade of trees *Tamus* extends about as far as *Melica uniflora* and *Sanicula* *europaea*, but remains flowerless there. Suppressed plants survive better under oak, ash, etc., than under beech and yew, probably because the shade is less deep.

The leaves are euphotometric, taking their position from the diffused light natural to the habitat (Burkill, 1944*a*).

III. *Communities.* Occurs in a wide range of woodland, thicket and hedgerow communities, all the common British trees providing suitable harbourage. Typical deciduous associates are *Quercus robur*, *Q. petraea* (*Q. sessiliflora*), *Fraxinus*, *Fagus* and *Carpinus*; *Taxus* and *Pinus* are evergreen associates. *Tamus* does not grow nearer than a metre to the trunk of *Fagus* and *Taxus*, the one deciduous, the other evergreen, showing that in Britain the winter condition of the sheltering tree is not of first importance.

No associate is more constant than *Quercus robur*, so much so that *Tamus* is markedly common in the oak-hornbeam and oak-ashwoods of the Midlands. *Quercus sessiliflora* is a less common associate, no doubt because *Tamus* and *Quercus robur* like similar soils. Similarity of soil preferences with the ash no doubt explains the fact that in the Derbyshire Peak *Tamus* ascends higher in the ashwoods than in the *Quercus sessiliflora* woods (Moss, 1913, p. 76).

Tamus cannot climb into large trees directly, as it has difficulty in climbing a pole over 5 cm. in diameter; if it begins, it falls off from over-curvature. When it does reach the lower branches, it is with the help of shrubs growing at the edge of the shade. The commonest supporting shrub in oakwoods is *Corylus avellana.* In mixed woods on the chalk the shrubs climbed are species such as *Acer campestre*, *Cornus sanguinea*, *Corylus avellana*, *Euonymus europaeus*, *Ligustrum vulgare*, *Rhamnus cathartica* and *Viburnum lantana.* Incidentally it is interesting to note that the leaves of *Tamus* are generally larger than those of the associated shrubs and their long petioles swing them into advantageous positions in front of the shrubs; the area of a typical *Tamus* leaf is 80 cm.^{2}, that of an abnormally big leaf over 200 cm.^{2} Thickets without large trees are as suitable as wood margins; the commonest shrub associates here are *Crataegus* spp. and *Prunus spinosa*. *Tamus* is not found in bramble patches, nor in Pteridietum, though *Pteridium* may invade thickets where *Tamus* grows.

In southern England the ground flora with which the seedling *Tamus* has to compete consists of grasses such as *Brachypodium sylvaticum*, *Melica uniflora* and probably *Arrhenatherum avenaceum*, and herbs such as *Anthriscus sylvestris*, *Galium mollugo*, *Geranium robertianum*, *Geum urbanum*, *Heracleum sphondylium*, *Melandrium dioicum*, *Mercurialis perennis*, *Nepeta glechoma*, *Ranunculus ficaria*, *Stellaria holostea*, *S. media*, *Stachys sylvatica*, *Urtica dioica*, *Viola reichenbachiana* and mosses, with trailing ivy and probably *Arum maculatum.* The seedling leaf among these thus faces considerable competition, but the older plant overtops this medley before any of the assimilating leaves expand.

On the Continent, *Quercus robur* is the chief associated tree as far east as the Alps, and even to the Caspian; other deciduous oaks such as *Q. cerris* and *Q. lanuginosa* are also associates. To the south of the Alps *Tamus* may have evergreen associates, e.g. *Quercus ilex* and *Q. suber*; it can climb into young trees of *Laurus nobilis* (Beck, 1901, p. 146). Thus, as in Britain, both deciduous and evergreen trees alike provide useful cover.

Tamus enters the *maquis* not only on the Adriatic coast, but in Corsica, Sardinia and Elba, where it is more typical: its associates here are very unlike its associates in Britain.

The boundaries of the distribution of *Tamus* are very like those of *Clematis vitalba*, but owing to the higher moisture requirements of the former, the two climbers very rarely intertwine. *Tamus* does not extend in Europe towards the north-east as far as any of the trees with which it is commonly associated in Britain, but is found beyond the southern limits of all of them. Part of its northern limit coincides with that of *Castanea vesca*; it grows in woods of this tree in the Balkans.

IV. *Response to biotic factors.* Thinning of woods is advantageous to *Tamus* by releasing suppressed plants. Trimming of hedges is also advantageous, even when done as late as between the hay and grain harvests, for if *Tamus* is cut while flowering, it recovers in the next season more rapidly than the hedge shrubs.

Tubers in thickets are often damaged at the head, obviously by the trampling of heavy animals; destroyed buds are replaced from the nearest convenient part of the tuber. Brenner (Lebensg. **1**, 695) claims to have got replacement in three weeks; usually, however, a year is lost (cf. Bucherer, 1889, p. 19). The rapidity of replacement seems to depend on the season at which injury occurs. Multiple stems often arise during replacement.

V. (*a*) *Gregariousness.* Plants are never so close—growing as to be gregarious, but stems of two plants may intertwine.

(*b*) *Performance in various habitats.* Brenner's data (Lebensg. **1**, 704) suggest that the plant produces a longer stem in Switzerland than in Britain (Burkill, 1936, p. 155), also that the tuber is larger (see VI (*a*), (*b*) below). Absence of flowering in deep shade has already been referred to; in Illyria, Beck (1901, p. 181) found flowering occurring in the shade of a *Ficus* which reduced the light to $\frac{1}{5}$–$\frac{1}{8}$.

(*c*) *Effect of frost, drought, etc.* Frost not uncommonly kills the ends of stems still in the soil and may injure the head of the tuber. The killing of the stem happens even in southern Devon; the nearest bud is then released for growth.

Tamus insures itself against droughts by water stored in the tuber and to a smaller extent in the ovary walls (Burkill, 1937, p. 67). The leaves are so much more resistant to drought than the leaves of the shrubs over which the plant has climbed that when plucked at the same time they wither after them. The whole plant contains mucilage which is tenacious of water (hence the German name *Schmerwurz*) and the very young parts are covered by minute several-celled hairs which cover the surface with slime when they burst.

VI. (*a*), (*b*) *Morphology of underground parts, etc.* The tuber of an old plant is a bulky body with its head 10–20 cm. below the soil surface. It may be 60 cm. long, but is generally scarcely more than 20 cm., though Brenner (Lebensg. **1**, 693) states that he has often found tubers 60 cm. long, weighing 10–15 kg., and with a diameter of 15–25 cm. The gradual sinking of the tuber in the soil is arrested by the roots which act as anchors even when dead. Sinking begins at the fall of the seed; wetting and drying of the seed causes alternating swelling and shrinking and in this way the seed works its way into the soil (Burkill, 1937, p. 35; for the structure of the seed-coat see Lebensg. **1**, 691). Owing to an after-ripening period before germination (see VIII (*j*)), there are 16 months on the average (minimum 6 months) during which sinking of the seed can take place. In the light loams of the Permian conglomerates of south Devon sinking averages 4·5 cm., but may be much more. The statement of Gardiner & Hill (1902, p. 445) that contractile roots produced on germination help to pull the young plant down is under investigation; whether it be right or wrong, the tuber soon begins to sink under its own weight. The apparent rising of the tuber when it sinks too deeply is not due to the roots pulling it up (Bucherer, 1889, p. 7), but to the growing out of a process from the tuber head (Lebensg. **1**, 695).

In the seedling the tuber arises as an acutely geotropic swelling, which enlarges on the lower side and acquires an apex of its own, descending year by year deeper into the soil. The initial stem is at its head and grows on sympodially by means of the first axillary bud of each successive year's growth. The primary root soon dies and the tuber comes to occupy its position. The tuber is at first white and of the same size as the seed (Fig. 1). A reddish brown covering of cork is formed before the second year. For a time the tuber remains globose, but in the third year it elongates and begins to have a firm corky crust. From its first year a cambium lays down parenchyma on its inner side; this is filled with starch and traversed by very small vascular bundles, by means of which, after the first three years, the age of the tuber can be estimated. The starch is never depleted during normal growth.

The roots on the tuber spread horizontally on all sides; those nearest the head of the tuber are longest, so that the top soil down to about 10–25 cm. is most explored. The roots spread to about 30–40 cm. In autumn they lose the cortex down to the endodermis, but the central cylinder lives on within a very strongly indurated double layer of cells (see Bucherer, 1889, fig. iv/4): this induration is characteristic of the Dioscoreaceae. These indurated roots last 5 years or more, but it is not known how long they remain alive; the growth of the tuber engulfs their bases.

(*c*) *Mycorrhiza.* Not detected.

(*d*) *Perennation.* Tuber geophyte. In Britain the nearest approach to rest is in October when the leafy stems begin to die at the base. As the stem dies, the bud in its lowest axil, which is virtually sessile on the tuber (indeed the tuber tends to engulf it), starts growth. Its lowest foliar organ is a calyptrate scale-leaf within which all its other parts are wrapped. The plant at this time is thus reduced to this bud (or there may be several), the tuber and the roots on the tuber.

(*e*) *Vegetative reproduction.* Reproduction by means of bulbils, so common in other Dioscoreaceae, does not occur. Vegetative reproduction can only occur by the accidental breaking of a tuber into parts, each one of which regenerates a bud.

(*f*) *Longevity.* Perennial. The age to which a tuber lives is not known. The rings of vascular bundles suggest that in southern England a tuber is 3 cm. in diameter at 15 years and 6 cm. at 30 years. The average large English tuber seems to be about 20 years old but Brenner (Lebensg. **1**, 693) has found tubers of 15–25 cm. diameter in Switzerland, which, if the increment is at the same rate as in England, must be much older than this.

(*g*), (*h*) *Age at first flowering and frequency of seed production.* Plants, if male and not suppressed, flower first when 5–6 years old; female plants flower a year or two later. Flowering and fruiting takes place every year. The male plant produces many more and larger inflorescences than the female from nearer the base of the stem; in England male plants carry about 30 times as many flowers as female plants and, as they are more numerous than the female plants, the proportion of male to female flowers is roughly 60 to 1. The female flowers, however, last about a day longer than the male flowers, so that the ratio of the two sexes open at one time is about 50 to 1.

(*i*) *Ecotypes.* No definite information, but variation in the shape of the leaf lamina may be in part ecotypic.

(*j*) *Chromosomes.* $2n=48$ (Meurman in Maude, 1939).

VII. *Phenology.* (*a*), (*b*), (*c*) The maximum growth of the tuber seems to occur about midsummer. The roots emerge from it contemporaneously with the shoot, elongating through the winter. Shoots come above ground in April and the leaves of mature plants expand at the beginning of May. The leaves of the seedling and young plant expand earlier than those of the mature plant. Flower buds at this time are fairly advanced and flowering begins at the end of May, lasting through June to the beginning of July. Flowering out of season has only been recorded once or twice in England, but may be more frequent in Switzerland (cf. Lebensg. **1**, 717).

(*d*), (*e*) After flowering the fertilized ovaries grow for about 80 days, then during about 20 more turn yellow and finally an exceedingly stable red. Disintegration begins inside by the three pads of water-holding tissue shrinking away from each other and from the epidermis: thereafter these pads and the ripened seeds lie in a watery juice within the tough epidermis. If protected from the weather they will continue so all winter. Exposed the berries become broken up in November and December by one cause or another, and the seeds scattered (Burkill, 1939, p. 49). If scattered late there is insufficient time for the process of after-ripening before the right temperatures for germination arrive in the spring, and germination is then delayed until a second winter has passed, i.e. for 16 months.

VIII. (*a*), (*b*) *Mode of pollination. Insect visitors.* The green flowers last $2\frac{1}{2}$–$4\frac{1}{2}$ days and are insect-pollinated. Forty-eight species of insects have been recorded as visitors (Burkill, 1944*b*, and additional records from E. A. Ellis), most of them inconstant and none, except perhaps *Anaphothrips tamicola* Bagnall, invariable; small bees seem to be useful agents. The visitors get honey in the faintly scented flowers. No fewer than 11 species of Empidae have been seen feeding in male flowers; it is suggested that they perforate the nectaries in doing so. The flowers belong to class 'B' (with hidden honey); the female flower faces more strictly towards the ground than the male, so an insect visiting it must be a little more adroit than on a male flower which faces obliquely downwards) except the terminal flower of one of the reduced inflorescences which appear with the latest leaves; this faces upwards). Many female flowers do not set seed, some because they fail to become pollinated, more because the development of the later pollinated flowers is arrested. The ovaries of unpollinated flowers enlarge for a time after flowering and then fall (Burkill, 1937, p. 66).

(*c*) *Cleistogamy.* Does not occur.

(*d*) *Apomixis.* Not recorded.

(*e*) *Vivipary.* Does not occur.

(*f*) *Hybrids.* None known. Carrière's record (1882, p. 379) of a hybrid with *Dioscorea opposita* produced naturally in a garden in France is indubitably an error. Hybridization might occur with *Tamus edulis*, a not fully distinct species of the Atlantic islands.

(*g*) *Amount of seed.* The 6 ovules in every ovary frequently all become seeds, but the average production in southern England is 3 (Burkill, 1937, p. 10). There is some reason for thinking that this arises by the sterilization of those seeds for which there is insufficient nourishment, rather than from failure of ovules to get fertilized. A large plant may produce about 1000 seeds in a season at the rate of 3 to a berry, but the average production is nearer 500.

(*h*) *Dispersal.* The berries are not a favourite food with birds, as they contain irritating raphides, a poisonous saponin, and but little sugar. The saponin probably repels the birds, but it diminishes in amount as the berries hang exposed to the weather (Burkill, 1937, p. 7). In England the missel thrush (*Turdus viscivorus* L.) and chaffinch (*Fringilla coelebs* L.) and in Switzerland the blackbird (*Turdus merula* L.) have been recorded as eating the berries. The mucilaginous juice within the berry makes the seeds sticky enough to adhere for a short time to a bird's bill or feathers and a bird feeding on the parenchymatous pads within the berry might unwillingly carry the seeds away. If swallowed the seeds would be uninjured owing to their hardness.

(*i*), (*j*) *Viability and conditions for germination.* Extensive sowings lead the writer to regard every seed produced as viable for a year, after which a falling off begins, but the maximum period of viability is unknown. The seeds require an after-ripening period which is terminated (i) by spring temperatures which induce germination, (ii) by drought which throws back the process to the beginning (Burkill, 1939, p. 44). An immense destruction of seed arises from this necessity of after-ripening for 6 months under moist conditions: the hedge of a ploughed field may be full of *Tamus*, so that an abundance of seed must reach the ploughed land, but a seedling never appears in it. There is no reason for thinking that light plays any part in germination.

(*k*) *Morphology of seedlings.* Seedling life lasts 3 (rarely 2) years. The cotyledon is a protuberance on the embryo which pushes the stem-apex aside and assumes the pole opposite to the primary root—the inner pole, as the embryo lies in a radius of the seed with its root end against the inside of the seed-coats. At germination the radicle lifts a little lid formed by the softening of a ring of tissue in the seed coats. As well as the radicle more of the embryo emerges, enough to free the stem-apex, leaving the greater part of the cotyledon inside. A minute tuber forms at the base of the cotyledon. Before germination the cotyledon, having pushed the stem-apex to one side, grows round it so that it lies in a pit. Just as the new stem each year ruptures the calyptrate scale-leaf, so the embryo plant stretches and destroys the wall of the pit. But before that happens the first assimilating leaf has been formed in the pit and it rapidly comes above ground after germination.

In the first year the seedling has a single assimilating leaf 10–18 mm. long, raised by its petiole usually 3–6 cm. above ground, though this can grow to 20 cm. with a part underground (Burkill, 1937, p. 37); the stem is completely suppressed. In subsequent years the stem is increasingly liberated and in the fourth year begins to twine. Flower buds may be laid down, but prevented from maturing, in the fifth or sixth year; a year later new buds may be matured. Other characters of the seedling stage can be seen in Fig. 2.

IX. *Parasites, diseases.* The plant has few insect enemies. The common cuckoo-spit insect, *Philaenus leucophthalmus* (L.) sometimes feeds on the leaves causing considerable distortion. A midge, *Schizomyia tami* Kieff., galls the male flower (H. J. Burkill, 1939, p. 34) and seems to extend right through southern England. Certain beetles feed on the pollen, destroying much of it. *Anaphothrips tamicola* Bagnall is possibly restricted to the plant and is very common: the injury it does is perhaps more than compensated by its assistance in pollination. The Psocopterid, *Graphopsocus cruciatus* (L.), may pass all its life up to maturity on the backs of the leaves, feeding on minute organisms and probably at the extra-floral nectaries, which lie chiefly near the junctions of the primary nerves, and does good rather than harm.

No serious diseases are known. The saprophytic fungus *Diaporthe scandens* S. & S. and its conidial stage *Phomopsis tamicola* Trav. (of which *Phlyctaena vagabunda* Desm. is probably an early stage) are associated with *Tamus*; *Cryptosporium tami* Grove is also peculiar to this host (Br. Stem and Leaf F. 1, 230). Three parasitic fungi have been recorded on the Continent as destroying the leaves and one has been found on the stems, but they have not been reported in Britain. Snails sometimes eat the margins of the leaves and the surface of the green berries, but never extensively. Baillon (1882, p. 334) recorded *Helix pomatia* L. in France, and the writer has seen *Cepaea hortensis* (Müller) and *Helicella virgata* (da Costa) in England and has fed parts of ripe berries to *Helix aspersa* Müller, which passes the raphides through its intestines apparently without discomfort (Burkill, 1937, p. 6). The saponin benumbs and may kill; it is undoubtedly protective against grazing animals.

X. *History.* The history of the genus *Tamus* may have been as follows. The parent genus *Dioscorea* had obtained a pan-tropical distribution when conditions began to lead to a segregation of its area into an eastern and a western half. *Tamus* emerged in the western half, the new genus being marked out by the development of water-storing tissue in the ovary walls, leading to a berried fruit. Fully effective bird dispersal was not attained. With the aid of the water storage tissues the plant was able to persist where it could endure a dry summer provided the winter rains were adequate. After the Glacial Epoch it spread northwards on that side of Europe where the winters were wet. Owing to its imperfect means of dispersal, it was unable to cross sea barriers and failed to reach Ireland till taken there a century back, or the Isle of Man (where it has been likewise introduced), though it reached England.

In Europe in addition to *Tamus* there are three other members of the Dioscoreaceae. The only other in western Europe is *Dioscorea pyrenaica*, which is nearly extinct; like *Tamus* it is derived from the western part of the *Dioscorea* area. In the Caucasus *Tamus* actually grows in company with *Dioscorea caucasica* (Radde, 1901, p. 52).

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REVIEW

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 12, No. 2, November 1943

This number of the *Journal of Animal Ecology*, somewhat delayed through the universal war-time printing difficulties, contains nine original articles, five reviews, and ninety-six Notices of Publications on the Animal Ecology of the British Isles. There are four papers dealing with ecological surveys of communities or groups of animals. K. A. Pyefinch's account of the intertidal and rock-pool habitats and their biotic communities on Bardsey Island contains matter of interest to plant as well as animal ecologists; taking the shore as including intertidal and rock-pools, there were 120 species of animals, whose rate of colonization of bare areas, and detailed ecology are discussed in relation to zonation and changes in the environmental factors. Following Macan's earlier work, E. J. Popham surveys the Corixidae (water-bugs) of a large number of pieces of water, correlating the colour acquired by each species, or possessed by it, with the colour of the natural background. Much of this coloration is determined in early life, through the eyes. The comparisons between the environment and the occurrences are quantitative. R. Erichsen Jones contributes a further paper in the important series dealing with the fauna of Welsh rivers in relation to river pollution from metal mines. The unpolluted River Teifi proved to have about 147 species of invertebrates and fish, nearly all typically stream species. The River Rheidol, which had previously been surveyed, as a river recovering from pollution, had a number of pool species in its fauna. M. K. Colquhoun and Miss Averil Morley carry the analysis of vertical zonation in woodland bird communities further, by counts of the vertical positions of tits and other small birds composing mixed winter flocks in an oak wood. Each zone was found to have its dominant species, and there was strongly marked differentiation between the blue tit (high) and the great tit (low zone).

W. Pickles, while serving with the R.A.M.C. in Algeria, was able to observe some interesting effects of variations in rainfall upon a small group of nests of the ant *Tapinoma nigerrima*, which requires mild rain to make the soil workable, but suffers from heavy rain, which destroys the work done. The series of papers on fish ecology, from the Freshwater Biological Association's laboratory at Windermere, is further enriched by a thorough study of the minnow (*Phoxinus phoxinus*). (This study coincided with, and largely is confirmed by, a parallel piece of work on the same species on the Continent.) It covers a wide field, including taxonomic characters of use in sex and age determination; scale readings for working out age-classes; conclusions about the rate of growth and length of life (up to three or four years); and an elaborate analysis of the food, evaluated from gut contents. The food studies again show the great variety of organisms eaten by such a general carnivore. The spawning habits and breeding season, movements and other ecology also receive attention. It is concluded that the minnow does not normally compete seriously with more valuable fish.

James Fisher and H. G. Vevers present a very complete and interesting study of the history and present breeding distribution of the gannet (*Sula bassana*), covering probably all the known 22 colonies, which are scattered over the coasts of the North Atlantic. A specially organized population count was made in 1939, which gave an estimated total population for this species of 165,600 ± 9500: one of the few approximations in existence for the total population of a comparatively abundant species. The paper is illustrated by some remarkable photographs taken by Coastal Command of the R.A.F., of breeding colonies on islands off Britain and Iceland, as well as by some other photographs and a map of the colonies. The literature is thoroughly reviewed, for the history of each colony, present or extinct. J. S. Watson gives a short note on the present existence of the black rat (*Rattus rattus*) on Lundy, a small island off Devonshire.

The results of the seventh annual Canadian Arctic Wild Life Enquiry are mapped and reviewed by Mrs Helen Chitty. They cover the season 1941–42, when arctic foxes were increasing or had reached a peak of their cycle over most of the Eastern Arctic of Canada, while lemmings had already begun to decrease, with a corresponding effect on that sensitive migrant, the snowy owl.

Reviews include the *Journal of Ecology*; the work of the San Joaquin Experimental Range in the Sierra Nevada, California (illustrated by two photographs, one showing the Upper Sonoran zone of vegetation); a Russian summary of work on methods of counting soil animals; a book on wild life in Great Britain; and a new American text-book of zoology. The Notices cover quite a surprising amount of good natural history and ecology, considering the effects of the War on field work and publication.

Charles Elton

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING IN THE UNIVERSITY DEPARTMENT OF BOTANY, OXFORD

5–6 JANUARY 1944

Wednesday, 5 *January*

The winter meeting of the Society was begun at 8.0 p.m. on Wednesday, 5 January, in the University Department of Botany, Oxford. About fifty members and guests enjoyed a pleasant social evening during which Mr H. N. Southern gave a most interesting lantern lecture upon the ecology of birds, and Dr W. O. James showed a film illustrating his own activities in directing a team of workers engaged in the collection of the drug plant *Digitalis.* There was opportunity during the evening to examine the exhibits set out to illustrate various aspects of ecology. Mr F. Ballard had set out a series of herbarium specimens, together with explanatory notes, of ferns used as food in different parts of the world: these included the well-known *Pteridium esculentem, Nephrolepis hirsutula, Marsilia minuta,* and the tree-fern *Cyathea medullaris* among others. Mr J. P. M. Brenan exhibited a series of herbarium specimens from west tropical Africa in illustration of his paper upon 'Macrophylly and Megaphylly', together with photographs to show the general habit of some of the species concerned. Mr C. E. Hubbard illustrated by specimens and comments a range of morphological complexity in the leaves and shoots of the Gramineae astonishing to botanists of restricted north-temperate knowledge of this family. Work done on behalf of the Ministry of Supply was illustrated by Dr V. J. Chapman's exhibit of the apparatus and methods evolved for algal surveys of extensive character upon rocky coasts. These demonstrated the feasibility of employing echo-sounding to give an outline of the main algal beds, and to distinguish between different kinds of bottom cover, and also showed the very great value of aerial photography in calm weather for such survey work. Dr E. W. Jones had set out the maps of oak woods in the Wye valley upon which he based his remarks as to the status of *Quercus robur* and *Q. sessiliflora* in the meeting next day. In the same way Dr N. Polunin showed specimens of the dwarf *Arenaria humifusa* of which he was speaking later. An exhibit of 'Hydrochasia', the interesting phenomenon of fruit dehiscence upon wetting, was made by Prof. T. G. B. Osborn, who encouraged members to experiment for themselves with the fruits of *Oenothera rosea.* He also showed tests proving the light-sensitiveness of the seeds of this species. Dr A. R. Clapham set out for inspection of members those parts of the Biological Flora already published, and the manuscript of the check-list now in preparation.

During the evening Mrs Osborn and friendly colleagues from the department provided refeshments on a pre-war scale of quality and quantity: by what means we cannot guess, but the society much appreciated them.

Thursday, 6 *January*

At 10 a.m. the next morning the Annual Business Meeting opened with the reading and signing of the minutes of last year's Annual Meeting, and with the reading of apologies for absence from Prof. Pearsall, Capt. Diver and Dr Watson.

The report of the Hon. Secretaries upon the work of the Society in 1943 was read and accepted in the form already approved by the Council.

Report of the Secretaries for the year 1943

The twenty-ninth Annual Meeting of the Society was held in the Botany School, Cambridge, on 5 and 6 January 1943. The meeting began with an afternoon assembly of members and guests at an extensive exhibit of ecological material: a lavish tea had been provided by our Cambridge hosts, or rather hostesses. At a soirée held the same evening in the Combination Room of Clare College between 80 and 90 members and guests were present: the Society's warm thanks to the Master and Fellows were expressed by Prof. Osborn. The business meeting was held next day at 10 a.m. and was followed by Dr H. Godwin's Presidential Address on 'Coastal Peat-beds of the British Isles and North Sea'. Other ecological papers followed in the morning and afternoon, the meeting closing at 4 p.m. We are very happy to thank Prof. Brooks and his colleagues for giving us the hospitality of the department, and help in organization of the meeting.

The Council has still found it impossible to arrange for a summer excursion, but in its place two most successful one-day meetings have been held. Both were in London. The first was held on Friday, 2 July, in the rooms of the Linnean Society, and took the form of a discussion on 'Ecological Principles involved in the Practice of Forestry'. Members of four forestry societies and the scientific staff of the Forestry Commission had been invited. The opening speakers were Prof. Tansley, Sir Roy Robinson, Prof. Champion and Dr A. S. Watt, and great interest was created by the meeting. We are very grateful to the Council of the Linnean Society not only for the use of their meeting room on this occasion, but also for the use of a committee room for our own Council meetings through the year. We are also grateful to the Royal Society for the use of a committee room on one occasion.

The second London meeting was held jointly with the Royal Entomological Society, in the rooms of that society in Kensington, on 12 November. The discussion was upon 'The Inter-relations of Plants and Insects; the place of both in the Ecosystem', and the chief speakers were Prof. Salisbury, Dr E. A. Cockayne, Capt. C. Diver and Dr C. F. C. Beeson. A full account of the joint meeting is being printed by the Royal Entomological Society, who are generously giving us the opportunity to buy sufficient offprints to circulate to our own members. Our particular thanks are due to Dr O. W. Richards who organized the meeting.

Again it has to be reported that publication of our journals is much delayed by war-time printing difficulties. Two numbers of the *Journal of Ecology* will shortly have appeared, containing respectively 108 and 162 pages. Six original papers with thirteen plates, together with reviews, notices and contributions to the Biological Flora will be contained in it.

Within a few days the second part of the *Journal of Animal Ecology* will also have appeared, making a volume of about 230 pages. The volume will contain 15 original articles, together with reviews. and the usual extensive list of notices of publications on the Animal Ecology of the British Isles.

To the Biological Flora accounts of four more species have been added, together with a carefully considered memorandum on Nomenclature and Taxonomy in the Flora. The preparation of many other accounts is now well advanced, and Dr Clapham is at work on a check list for use with the Flora. It is now four years since the Society decided to undertake publication of the Flora, and thanks to the devoted labour of the three editors appointed to launch it, Dr Clapham, Dr Richards and Prof. Pearsall, we can say that the project has been very successfully begun. The Council has decided upon a three-yearly appointment of editors for the Flora, and has now reappointed the three initial editors for that term.

In view of the interest in national post-war planning, and in particular of the importance of an ecological approach to problems of nature conservation, the Council, in May 1942, appointed a sub-committee to consider and report on the matter. After very careful inquiry, formulation and modification, the report as finally drafted by the convenor, Prof. A. G. Tansley, has been approved by the Council for publication in the journals: copies have been widely sent to suitable authorities and persons concerned with post-war planning, and to suitable journals for review. Copies are on sale by the Cambridge University Press.

The sub-committee has also compiled, with the assistance of many of the Society's members, a list of areas recommended for conservation. The appropriate sections of this list have been sent to the convenors of local sub-committees of the Nature Reserves Investigation Committee. A separate list of proposed National Reserves was also drawn up and circulated to members of the Nature Reserves Investigation Committee itself.

During the year the membership of the Society has risen from 378 to 398 members, 12 members having resigned or died, and 32 new members having been elected. Of the present membership 216 receive the *Journal of Ecology* alone, 127 the *Journal of Animal Ecology* alone, 53 take both journals, 2 neither.

H. Godwin } *Hon. Secretaries*
L. A. Harvey }

Mr V. S. Summerhayes then gave a provisional estimate of the financial position of the Society. Though hampered by the lateness of printing and presentation of bills, he suggested that the Society would probably close the year with a credit balance of about £100 on the year's working, and this despite the increased expenditure consequent upon the work on Nature Conservation enquiry. Both he and Dr Watt urged a further extension upon members of the practice of using Banker's Orders for payment of subscriptions. It was proposed by Mr Summerhayes, seconded by Dr Watt, and carried unanimously, that a grant of £10 be made to the Freshwater Biological Association in 1944. On the proposal of Dr Turrill it was agreed that Messrs Wm. Norman and Sons be reappointed auditors to the Society, and the very cordial thanks of the meeting were accorded to the two Hon. Treasurers for their unremitting and remunerative labours.

Dr A. R. Clapham, on behalf of the editors of the Biological Flora, explained the present satisfactory position of accounts in preparation, and of the work in hand upon a check list.

The meeting then proceeded to the election of officers as follows:

President: O. W. Richards.
Vice-Presidents: A. G. Tansley, C. Diver.
Hon. Secretaries: H. Godwin, L. A. Harvey.
Hon. Editors: W. H. Pearsall, C. Elton.
Ordinary Council Members: T. A. Stephenson, R. C. McLean, G. H. Champion.
(Retiring Council Members: A. Foggie, J. Ritchie, T. G. B. Osborn.)

The new President then took the chair and Mr Harvey announced that a Symposium had been arranged upon 'The Ecology of Closely Related Species', that it would be held at Easter in London, and that Mr Lack, Dr Varley, Capt. Diver and Mr Elton had undertaken to speak.

Prof. T. G. B. Osborn then gave his paper upon 'Edaphic Climaxes in Australia', illustrating by lantern slides the very great differences in vegetational type which often occur within short distances, and which are evidently caused by edaphic differences, for example open desert scrub of *Acacia aneura* and *Cassia* spp., meeting the dense thicket of *Triodia* where the soil changes from deep sand to a soil with limestone concretions. Similar effects were shown where basaltic flows occur near Melbourne, and where, near Sydney, Triassic shale and Hawkesbury sandstone meet. Dr Turrill, Dr Watt, Miss Moore and Dr Polunin took part in the discussion raised by Prof. Osborn's interesting thesis.

The next paper was by Mrs J. Fitzpatrick, upon 'The Ecology and Cytology of British species of *Glyceria*'. Somatic chromosome counts by the author gave the following results: *G. declinata* $2n=(20)$; *G. plicata* $2n=40$, *G. fluitans* $2n=40$, *G. maxima* $2n=c.\ 60$, *G. plicata* × *fluitans* $2n=40$. Of these species *G. declinata* is the most drought-tolerant, living in dried-up ponds of temporary character, *G. fluitans* is found in the wettest places, such as streams and ditches, whilst *G. plicata* and the hybrid favour stations of intermediate wetness. In the discussion which followed Mr Hubbard gave several reasons for thinking that *Glyceria* might have had a tropical origin and be connected with the Oryzeae. Dr Turrill, Mr Simmonds, Mr Brenan, Mr Pentelow and Dr Polunin also took part in the discussion.

Mr D. H. Chitty continued with a paper on 'The Population Cycle of the Canadian Snowshoe Rabbit, *Lepus americanus*', an animal of very great importance as food for the fur-bearing carnivores and as an agent destructive of plant life. He was able to show that the showshoe rabbit population has a pronounced cyclic fluctuation with a period of 9–11 years, which is followed after a three years' lag by the cycle of lynx, an animal almost wholly dependent on the rabbit for food. The data brought out the interesting fact that the cycle was not exactly in phase in different parts of North America, so that for instance the population in 1937–8 was recovering in the east whilst still minimal in the west. Mr Chitty commented on possible mechanisms by which the cycle might be determined, and this led to a prolonged and valuable discussion in which the following took part: Dr Clapham, Mrs Harvey, Mr Spooner, Mr Lack, Dr Watt, Dr Polunin, Dr Jones, Dr Hope-Simpson and Dr Turrill.

Mr J. P. M. Brenan then gave an account of macrophylly and megaphylly in the woody species of tropical West Africa. He was concerned with plants of the rain forest and of dry savannah. It was pointed out that shrubs and small trees are very heavily represented in the big-leaved classes, especially where the leaves are in terminal rosettes, and the stems are little branched so as to give the *Schopfbaum* habit. The large leaves are rare in the tall trees of rain forest and contribute little to its physiognomy, but more often is associated with shrubs and small trees of lower storeys. It is a habit found in many distinct families, and a tendency towards it is recognizable also in species with compound leaves. Dr O. W. Richards, Dr Clapham and Dr Hope-Simpson took part in discussion of the paper.

After the adjournment for lunch, Dr H. Godwin took the chair in the absence of the President and called on Dr Turrill for his paper on 'Vegetation from the Military Standpoint'. Dr Turrill discussed the kind of information which plant ecologists might be asked to give to military authorities in war-time. The area, density, tallness of different communities had to be given, the tallness and extent of tree canopy, penetrability to men and vehicles of various kinds, the obstacles presented by climbers and spinous plants, by bogs and dunes, together with data on the way in which seasonal changes might affect the operation of these factors. He stressed the value to the compiling ecologist of clear descriptive accounts, with measurements, of vegetational maps of territory actually worked over, and of fully annotated photographs. He pointed out that suitable material had not been prepared before the war. Dr Clapham raised questions after the lecture.

The next paper was read by Dr N. Polunin upon 'The Phytogeographical Insignificance of *Arenaria humifusa*'. The object of the paper was to stress the need for caution by phytogeographers in drawing conclusions based upon the *absence* of a given species from any area. *Arenaria humifusa* is a very small boreal species cited 20 years ago by Fernald as a per-glacial survivor, and more recently also regarded by Nordhagen as having relic distribution in Scandinavia. Dr Polunin pointed out that not only is this species very inconspicuous, but that we know nothing as to how easily it may be dispersed by birds or other means, adding that the number of major regions where the species grows has been almost doubled since Nordhagen wrote. The need for caution in accepting insignificant plants as absent is emphasized by the recent discovery in the Hebrides of *Carex bicolor*. Questions were put after the lecture by Mr Elton, Dr Turrill, Dr Clapham and Miss Gibson.

The last paper of the meeting was that given by Dr E. W. Jones on 'The Distribution of the two British Species of Oak, *Quercus robur* and *Q. sessiliflora*'. Of the two factors of soil and climate generally invoked to explain the different distribution of these species he did not find the soil factor very recognizably effective. Whilst rare in the Midlands, *Q. sessiliflora* entered abundantly along a line west of the Severn. By careful consideration of the estate records for woodlands near Symond's Yat he showed that the earliest woods there were all *Q. sessiliflora,* whilst later plantings have included a greater or less percentage of *Q. robur.* It seems clear that selective planting and felling has played a big part here as in the Scottish woods described by Dr Wyllie Fenton, and Dr Jones, who is preparing accounts of the two oaks for the Biological Flora appealed to members to assist him as fully as possible by collecting data on distribution. A full discussion followed in which Dr Godwin, Dr Richards, Mr Elton, Mr Tutin, Dr Clapham, Miss Lambert and Mr Lack spoke.

The chairman brought the meeting to a close by offering the heartiest thanks of the Society to Prof. Osborn and his staff for having once again afforded an exceptionally pleasurable opportunity for the Annual Meeting. The meeting cordially acclaimed these sentiments.

LIST OF MEMBERS (1 March 1944)

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VEGETATION OF ROYDON COMMON

BY C. P. PETCH

Roydon Common is one of the many tracts of heath on the range of Lower Greensand hills that border the eastern shore of the Wash. Similar areas are found in the parishes of Dersingham, Wolferton, West Newton, Wootton and Leziate. The district is one of the driest in the British Isles with an annual rainfall of less than 25 in. (63 cm.). The altitude is nowhere great enough to affect the vegetation which is determined locally by the soil. The Common itself occupies an area of nearly 2 sq. miles, roughly two-thirds being elevated and dry, the remaining third low-lying and boggy. It is not subjected to any kind of grazing, but sporadic fires sweep over the drier parts. Rabbits are numerous.

DRY AREAS

The dominant plants are *Calluna vulgaris* and *Pteridium aquilinum.* In the more inaccessible portions, and on the peninsulas which project into the bog, pure Callunetum is found. In other places, particularly towards neighbouring arable land, *Pteridium* is the sole dominant. Over very large areas, however, the two plants exist side by side in varying proportions. It appears that burning favours *Pteridium* at the expense of *Calluna**. The marked sample which escaped burning during seven years over which observations were made showed a very distinct lessening in the number of bracken fronds, though the plant had by no means disappeared. It seems probable that in the absence of fires *Calluna* would eventually exclude *Pteridium,* though the process would be very slow. The spread of bracken is strictly limited by the bog. The lowest level reached by the plant, as determined by observations on the water table in pits, corresponded to water at about 3 ft. (1 m.) from the surface in summer. It may, however, be the higher level of winter waterlogging that operates as a restricting factor.

Associated plants in this community are few. The heaths of north Norfolk on glacial gravels bear *Ulex minor* and *Erica cinerea* abundantly in the Callunetum, but these are not found here. Some pure societies of *Carex arenaria,* reaching a maximum of 50 m. in diameter, exist in association with rabbit burrows. *Cuscuta epithymum* is frequent on the heather in the late summer. Grass heath plants (vide infra) and *Tillea muscosa* occupy the paths. Fringing the bog, though not in it, are *Genista anglica, Pedicularis sylvatica* and *Juncus squarrosus.* Fires have the effect of causing these to spread temporarily into the Callunetum, in company with several of the bog species. *Epilobium angustifolium* also appears sporadically after fires. In one place, on the slopes of a hill, *Scilla non-scripta* is found beneath the bracken and may represent a relic of former woodland. There has been no evidence of tree or shrub colonization of the dry areas during the period of observation, though similar tracts of land elsewhere in west Norfolk are colonized by birch. Birch trees on dry land at Roydon are only seen adjacent to two of the larger areas of carr, from which they appear to have spread. These trees, however, tend to suffer very severely from burning, and it is presumably this that prevents their further extension.

The most interesting feature of the common is a patch of bent-fescue grassland, or grass-heath, occupying about 50 acres on the highest part of the dry area, and standing

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* The latter regenerates freely from seed, the former from rhizomes.

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out in sharp contrast to the Callunetum. After an unsuccessful search for soil differences it was realized that the grass-heath owed its origin to former cultivation, although it had not been ploughed since 1918 (written in 1941). It represents in fact an old field whose boundaries are visible in the form of a shallow ditch. It is apparent that *Pteridium* and in one place *Calluna* have invaded the former cultivated area, but the surprising feature is the small extent to which this has occurred: *Pteridium* has reached a maximum of 135 m. from the ditch and no advance was detected during the period of observation (1934–40). The following species are found in the grass-heath:

Festuca ovina	co-d.
Agrostis alba	co-d.
A. canina	o.
Aira praecox	a.
Alchemilla arvensis	a.
Anagallis arvensis	o.
Arenaria serpyllifolia	f.
Cerastium arvense	f.
C. semidecandrum	a.
Cnicus repens	f.
C. lanceolatus	o.
Carex pilulifera	f.
Campanula rotundifolia	r.
Cynoglossum officinale	n.
Draba verna	a.
Erodium cicutarium	f.
Erythraea centaurium	o.
Filago minima	o.
Galium saxatile	r.
G. verum	r.
Geranium molle	a.
Hypochaeris glabra	o.
Luzula campestris	l.f.
Lycopsis arvensis	r.
Myosotis arvensis	r.
M. versicolor	a.
Nepeta hederacea	l.f.
Plantago coronopus	r.
Rumex acetosella	a.
Sagina procumbens	f.
S. apetala	f.
Saxifraga tridactylites	o.
Senecio campestris	f.
Stellaria media	l.
Sedum acre	r.
Solanum nigrum	v.r.
Taraxacum officinale	r.
Teucrium scorodonia	l.d.
Teesdalia nudicaulis	r.
Urtica urens	o.
U. dioica	f.
Veronica arvensis	r.
Viola riviniana	r.

Some of these, e.g. *Anagallis arvensis* and *Lycopsis arvensis*, may owe their introduction to cultivation. No fires have been seen in or near the grass-heath: the grass is too short to burn and too scanty for grazing. The soil is for the most part pure sand exactly similar to that of the Callunetum except that the latter shows the development of a B horizon which is lost in the former. As has already been stated, it is not possible to correlate the different dominants with soil differences, but edaphic factors show their effect in the following way. In one corner of the grass-heath a deposit of chalky boulder clay is found near to the surface, overlain by only 9 in. (22·5 cm.) of sand in the shallowest parts. Samples of this sand from just below the surface showed marked effervescence with hydrochloric acid. It is in this locality that invasion of the grass-heath by *Calluna* as opposed to the more usual *Pteridium* has occurred, a fact which may be due to the shallowness of the sand preventing the development of bracken rhizomes. Here too the bent-fescue society of the grass-heath is enriched by the development of the following species, which are not found elsewhere:

Cerastium vulgatum	a.
Carlina vulgaris	l.f.
Calluna vulgaris	o.
Hypochaeris radicata	o.
Hieracium pilosella	l.f.
Holcus mollis	a.
Hypericum humifusum	f.
Lotus corniculatus	r.
Leontodon officinale	f.
Prunella vulgaris	f.
Potentilla fragariastrum	r.
P. tormentilla	r.
Plantago lanceolatum	r.
Ranunculus repens	a.
Trifolium repens	r.
Veronica chamaedrys	o.
V. officinalis	f.
V. serpyllifolia	f.

The improvement of the soil by the underlying chalk seems responsible for the presence of these plants, but it is noteworthy that they are associated with healthy *Calluna*. In this region also are two small pits, now with permanent water, which were presumably dug as marl pits. The deeper one is dominated by *Potamogeton natans* and *Typha latifolia*, the shallower by *Equisetum limosum*. They contain twenty-seven species of common aquatic plants of neutral waters remarkable only in their contrast to the bog vegetation with which they have no species in common.

Some light is thrown on the relation between grass-heath and arable land by the fate of two sandy arable fields on a nearby farm which went out of cultivation during the period of these observations. In each case bracken spread from the border of the field during the first few years, while the centre was occupied by arable weeds and ephemerals. After a few years a relatively stable state was reached, with a marginal fringe of bracken surrounding a large area of grass-heath with a flora similar to that already listed. If, as seems to be the case, the grass-heath on the common arose in a similar way, this state of affairs persists under suitable conditions for over twenty years. It will be remembered that there is no grazing apart from that done by rabbits. Temporary cultivation of heathland is not rare in East Anglia: the word 'breck' is used to denote fields made in this way. Little note has been taken, however, of the long lasting type of grassland which arises on these barren soils after such operations.

WET AREAS

The vegetation of the wet areas has the nature of a valley bog developed in a region of impaired drainage with soil water lacking in mineral salts. Peat is from 9 to 18 in. deep (22·5–45 cm.). *Erica tetralix* is universal but occupies hummocks and small elevations, the hollows being filled by *Sphagnum* and *Narthecium ossifragum*. *Scirpus caespitosus* is common and spreads into the Callunetum after fires, which burn down to the edge of the bog but not as a rule over it. Where the peat is deeper the taller *Junci*, *Molinia caerulea*, *Phragmites* and *Myrica gale* mark the transition to carr. A small society of *Cladium mariscus* exists near the eastern boundary ditch, but the plant is not typical. The bog vegetation, and to a lesser extent the carr described below, covers a large part of the north-eastern half of the common, and a smaller isolated tract near the southern border. Outside the boundary ditch or fence of the common, the enclosed fields adjacent to the wet areas are coarse pastures, presumably developed from the bog by drainage and grazing. Many species are common on both sides of the boundary (e.g. *Juncus sylvaticus*, *Potentilla erecta*, *Scabiosa succisa*), but the most characteristic bog species (*Erica*, *Narthecium*, *Drosera*, etc.) are not found in the pastures. A list of the bog flora follows:

Erica tetralix	d.
Molinia caerulea	l.d.
Sphagnum spp.	l.d.
Arundo phragmites	l.a.
Anagallis tenella	r.
Calluna vulgaris	f.
Cnicus anglicus	l.f.
Carex flava	r.
C. echinata	r.
C. panicea	o.
Cladium mariscus	l.f.
Drosera rotundifolia	f.
D. anglica	o.
D. longifolia	o.
Eriophorum angustifolium	a.
E. vaginatum	v.r.
Habenaria bifolia	r.
Hypericum elodes	r.
Juncus sylvaticus	l.a.
Juncus bulbosus	o.
Myrica gale	l.a.
Malaxis paludosa	v.r.
Narthecium ossifragum	a.
Orchis incarnata	r.
Pedicularis palustris	r.
Pinguicula vulgaris	r.
Polygala vulgaris	r.
Potamogeton polygonifolius	r.
Potentilla tormentilla	f.
Rynchospora alba	l.a.
Scabiosa succisa	l.f.
Schoenus nigricans	l.a.
Scirpus caespitosus	f.
S. multicaulis	o.
Salix repens	o.
Utricularia intermedia	r.
U. minor	l.f.
Vaccinium oxycoccos	a.

CARR

As has been already stated, the wetter parts of the bog support *Myrica gale* and taller marsh plants. Fires do not occur here. As the peat deepens the drainage water collects into definite channels, and birches, sallows and *Frangula alnus* appear. Finally, around the streams which drain the bog there grows a dense thicket, locally known as carr, whose floor, wet in the driest seasons, bears a rich and varied marsh flora. Some of these plants are definite shade lovers, while others are marsh species that will not tolerate the more acid conditions of the bog. There is considerable local variation in the ground layer, which is made up sometimes of tussocks of *Carex paniculata*, and others of sheets of *Hydrocotyle vulgaris* or beds of rushes, but there is a remarkable constancy of species between the carrs. This development has taken place in several separated localities, giving thickets of varying extent. From two of them, as has already been observed, birch trees have spread on to adjacent dry land. The ground flora here is of course not that of the carr but consists of *Pteridium*, *Teucrium scordonia*, *Galium saxtile* and other shade-tolerant heath species with the addition of *Rubus fruticosus*, *Corydalis claviculata*, *Campanula rotundifolia* and a few others.

During the period of observation no increase in the dry area covered by trees has been noted. Burning seems the most obvious factor preventing their spread.

Carr flora

(1) *Trees and shrubs:*

Betula alba	d.
Lonicera periclymenium	f.
Myrica gale	a.
Populus tremula	r.
Quercus pedunculata	l.a.
Frangula alnus	f.
Rubus fruticosus	o.
R. idaeus	o.
Rosa spp.	r.
Ribes nigrum	r.
Salix aurita	a.

(2) *Ground layer:*

Arundo phragmites	f.
Angelica officinalis	o.
Cnicus palustris	f.
Calamagrostis lanceolata	o.
Carex paniculata	o.
C. echinata	o.
Caltha palustris	o.
Equisetum palustre	f.
Epilobium tetragonum	f.
Galium uliginosum	o.
G. palustre	r.
Hydrocotyle vulgaris	a.
Holcus lanatus	a.
Juncus conglomeratus	f.
J. effusus	o.
J. sylvaticus	a.
Lythrum salicaria	o.
Lychnis flos-cuculi	o.
Lastrea thelypteris	f.
L. dilatata	o.
Lycopus europaeus	r.
Lotus uliginosus	f.
Mentha aquatica	a.
Menyanthes trifoliata	r.
Molinia caerulea	a.
Osmunda regalis	v.r.
Orchis elodes	r.
Potentilla palustris	o.
P. tormentilla	o.
Ranunculus flammula	o.
Solanum dulcamara	o.
Scabiosa succisa	o.
Valeriana dioica	o.
Viola palustris	o.

SUMMARY

A description is given of the vegetation of a common in west Norfolk, part dry heath and part bog, over a period of ten years. Attention is drawn to the remarkable persistence of the grass-heath which follows the abandonment of cultivation.

FIGYN BLAEN BREFI: A WELSH UPLAND BOG

BY E. G. DAVIES

(*With Plate* 1 *and eight Figures in the Text*)

INTRODUCTION

The bog at Blaen Brefi, near Llanddewi Brefi, Cardiganshire, is situated some 25–30 km. inland, at a height of approximately 410 m. (1350 ft.) above sea-level, in a declivity between two hills, which themselves form a wind corridor running north-west to south-east. The bog forms the gathering ground of two rivers, the Afon Brefi, which drains the greater part of the area, and runs north-west, and the Pysgotwr Fawr, which flows to the south-east.

TOPOGRAPHY AND GEOLOGY OF CARDIGANSHIRE

Cardiganshire possesses an exposed windswept seaboard, with a hinterland rising, more or less gradually, to an exposed elevated plateau, 395–550 m. (1300–1800 ft.) above sea-level, intersected by numerous sheltered valleys. The coastal plateau, which stands uniformly at a lower level, is separated from the high plateau by a fairly marked rise or shelf, which, it has been suggested, marks the position of an ancient coastline.

Geologically, the county consists almost entirely of grits and shales of the Ordovician and Silurian series. Limestone is practically absent, and even the boulder clay is non-calcareous. The grits are harder than the shales, and therefore tend to form the higher ground of the plateau.

The geographical history of Cardiganshire has its bearing upon the present plant distribution. According to O. T. Jones (1911) at some time in the Tertiary period, the area bordering on the present coast was reduced by denudation to a surface of low relief. Subsequent uplift raised it some hundreds of feet above sea-level, and, in this uplifted plain, the present rivers cut steep-sided narrow valleys, the mouths of which were at a grade with the new level of the sea.

Erosion during the glacial epoch modified slightly the form of the valleys, especially those which lay in the direction of the ice movement. After the retreat of the ice, the valley floors and, probably, much of Cardigan Bay, were covered with boulder clay. The latter also covers considerable areas on the coastal plateau, and upland peat deposits are found overlaying the boulder clay on the hilltops and in the hollows of the high plateau.

CLIMATE

A brief general description of the climate of the county is a useful contribution to the understanding of some of the factors influencing plant distribution in the special area under investigation. Cardiganshire, with its exposed, windswept seaboard, experiences a small mean annual range of temperature, and a fairly high rainfall (Jones, 1931; Air Ministry, 1940). The climate of the district is one of cyclonic control, with a corresponding irregularity in wind direction and force. This fact is held responsible for the rapid daily fluctuations in temperature. The classical example of this phenomenon is taken from the

Aberystwyth station, where the total annual range of temperature is 17·3° (Air Ministry, 1933). Records taken by the Harbour Master, Aberystwyth (1938), in December 1938, show that in 48 hr. the total annual range can be experienced. Owing to these considerable variations from day to day, together with the small temperature range, the conditions at any time, in any season, might revert to those of the preceding season, or might anticipate the succeeding season. The unreliability of the seasons with regard to temperature is important, because temperature, to a large extent, controls the growing seasons.

Owing to the inaccessibility of Blaen Brefi, actual figures for the rainfall cannot be given. On the basis of existing records, it cannot average less than 55 in. (140 cm.) per annum, reaching a maximum in autumn and winter. High rainfall in July and August is a normal feature, the summer months being characterized by heavy showers. The rainfall during the winter months is cyclonic precipitation, which at Blaen Brefi is subject to orographical influence. The summer rain is mainly convectional in character, and the rate of fall is greater than in cyclonic or orographical rain. The summer and winter types of rainfall have markedly different effects. An example of the effects of summer rainfall was seen at Blaen Brefi on 16 July 1939, when a thunderstorm accompanied by a cloud-burst caused severe landslides along the valley sides of the Afon Brefi. Such storms have a marked effect on peat areas, since they result in the washing down of large quantities of peat by the streams.

Precipitation in the form of snow is a feature of the high plateau during the winter months, and its influence in connexion with the erosion of peat lands is very marked when the spring thaw sets in.

The autumn and winter seasons show a combination of short days and overcast skies. Most sun is seen in the early summer, but even then the sunshine hourage is considerably smaller on the high plateau than it is in the coastal regions. An important feature of high inland regions in this part of Cardiganshire is the cloud cover. Frequent cyclonic disturbances cap the hills with clouds which cover them for several days, although actual precipitation may not take place. This condition is frequently observed at Blaen Brefi at all seasons, and is so marked at times that visibility is practically nil. Such a phenomenon influences light and temperature, as well as atmospheric humidity, and is therefore bound to have an important effect on vegetation.

Over the greater part of the year, the prevailing direction of the wind is from the south-west and south, but winds from other quarters are by no means infrequent. In early spring (February to April), however, there is a seasonal maximum from the east, north-east, and north. Winds with an easterly component are common in all months. Blaen Brefi is sheltered, to some extent, by the low hills to the south and west, and by those to the north-east. In spite of this, however, the region is one which experiences very strong winds, especially from the north and south-east. The narrow valleys of the Afon Brefi and Pysgotwr Fawr form 'corridors' which tend to accentuate wind force and, to a large extent, control wind direction. In such high mountain regions with narrow valleys, wind direction near the ground appears to depend largely on the relief. At such high altitudes the wind is likely to have great effects on the vegetation, and it is here that the efficiency of wind as an agent of erosion is seen at its maximum.

The vegetation at Blaen Brefi may be said, therefore, to be influenced by cool summers, mild winters, heavy rainfall, very high atmospheric humidity, and very strong winds.

METHODS

After having made a primary reconnaissance to ascertain the distribution of the main plant communities and other features of interest, a more detailed study of the surface ecology of the bog was undertaken. The floristic composition and structural features of the communities were ascertained by means of transects and quadrats, the two latter being laid down after a grid system had been constructed. Percentage transects for which the grid lines formed a basis, were used in place of the more familiar line transects. The data were obtained from the examination of belts 10 m. in width on both sides of the grid lines. Chart quadrats were also made of selected characteristic areas. From all the data thus obtained, the map in Fig. 1 was constructed. By a process of levelling, the general configuration and variations of slope were determined, while borings made at intervals along predetermined lines enabled the depth of the peat above the underlying clay to be ascertained. The records are shown in Figs. 2 and 3. The general nature and composition of the peat was observed when borings were taken, and a more detailed examination was made at particular points, as shown in Fig. 4.

SURFACE ECOLOGY OF BLAEN BREFI

From the data obtained by means of transects and quadrats the distribution and composition of the plant communities may be considered. The distribution of the principal communities is clearly seen at all seasons, but particularly so in autumn and winter, when the zonation presents itself as a distinct colour difference.

In general, the bog may be said to occupy a shallow basin between two lines of hills, which themselves are covered with rough mountain pasture dominated by *Molinia* tussocks, often with abundant *Polytrichum commune*. On this pasture, sheep, and less often, cattle, graze. The grazing, however, has not caused the bog to be delimited sharply from the pasture land. There is little peat cutting—though a small area in the south-east has been cut.

A general survey of the surface ecology shows that the vegetation of the bog itself may be divided broadly into three zones (Fig. 1 and Pl. 1, phots. 1 and 2). The centre is occupied by an erosion complex (using Osvald's terminology), which is adjacent to a wide Scirpetum on the north side, and a similar smaller area on the south-west. The Scirpetum merges into a Molinietum whose continuity with the *Molinia* pasture of the hills is broken only by the *Juncus* strips at the base of the hills and areas of Juncetum in the north and north-east.

The detail, however, is not quite as simple as might appear from the general survey. Adjacent to the erosion complex on the south and west, a wet area of Sphagneto-Juncetum occurs, while to the south-east a mixed Molinietum-Juncetum may be seen.

The different communities are widest where the basin is widest; where the hills converge the zones are much narrower.

EROSION COMPLEX

This zone is characterized by large, dry depressions in the peat, separated by large hummocks (Fig. 5). These topographic forms have no definite orientation, and are irregularly placed. In the central portion of the complex, the hummocks and depressions occupy approximately equal areas. These facts can be correlated with the development

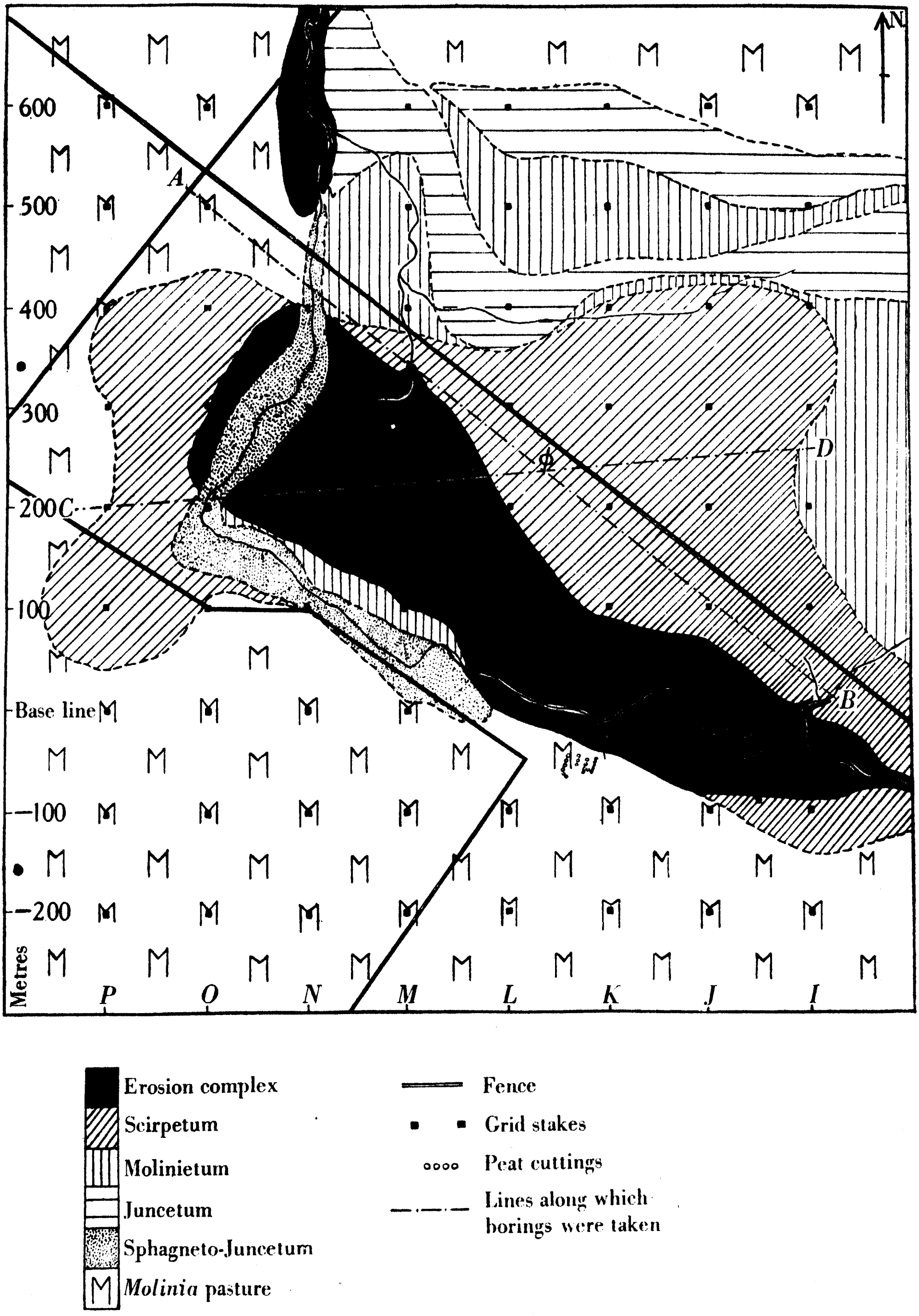


Fig. 1. Figyn Blaen Brefi. Map showing distribution of vegetation.

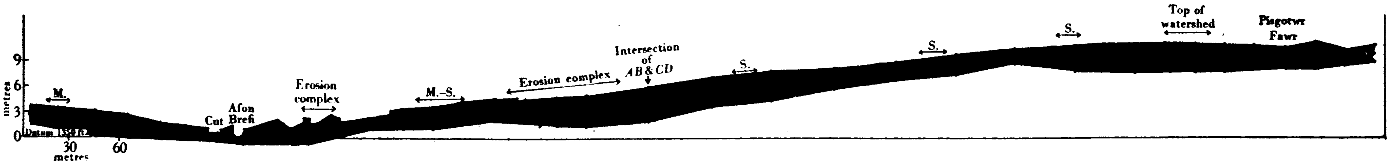


Fig. 2. Configuration of bog as determined by levels and borings along line *AB* in Fig. 1. Peat in black.

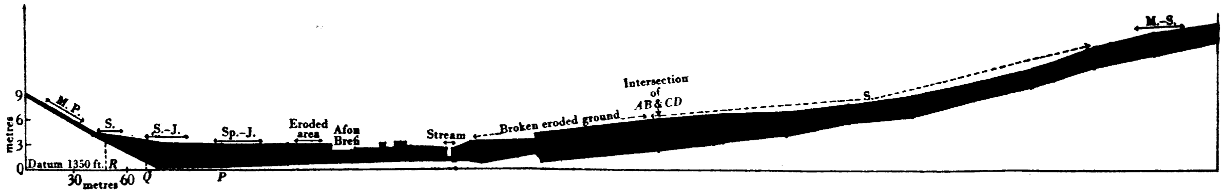
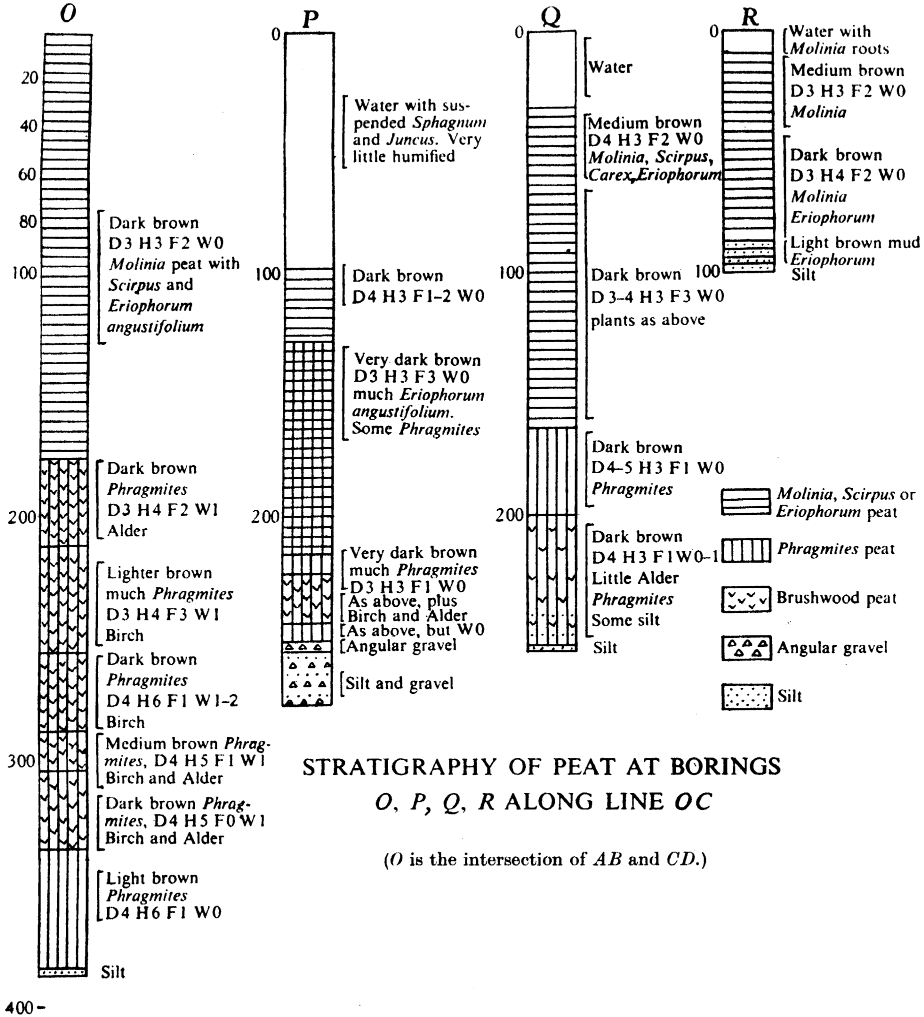


Fig. 3. Configuration of bog as determined by levels and borings along line *CD* in Fig. 1.

Key to Figs. 2 and 3

M.	Molinietum.	M.P.	*Molinia* pasture.	M.-S.	Molinietum-Scirpetum.
S.	Scirpetum.	S.-J.	Scirpetum-Juncetum.	Sp.-J.	Sphagneto-Juncetum.

of the erosion complex from a comparatively level area of bog. At the south-eastern side there is an increased slope to which the depressions tend to lie more or less at right angles. In this region, however, a great deal of erosion has taken place, so that the ratio depressions/hummocks is very high, and in consequence the orientation is often difficult to determine.


O
P
Q
R
0
20
40
60
80
100
200
300
400
Dark brown D3 H3 F2 W0 *Molinia* peat with *Scirpus* and *Eriophorum angustifolium*
Dark brown *Phragmites* D3 H4 F2 W1 Alder
Lighter brown much *Phragmites* D3 H4 F3 W1 Birch
Dark brown *Phragmites* D4 H6 F1 W1-2 Birch
Medium brown *Phragmites*, D4 H5 F1 W1 Birch and Alder
Dark brown *Phragmites*, D4 H5 F0 W1 Birch and Alder
Light brown *Phragmites* D4 H6 F1 W0
Silt
Water with suspended *Sphagnum* and *Juncus*. Very little humified
Dark brown D4 H3 F1-2 W0
Very dark brown D3 H3 F3 W0 much *Eriophorum angustifolium*. Some *Phragmites*
Very dark brown much *Phragmites* D3 H3 F1 W0
As above, plus Birch and Alder
As above, but W0
Angular gravel
Silt and gravel
Water
Medium brown D4 H3 F2 W0 *Molinia, Scirpus, Carex, Eriophorum*
Dark brown D 3–4 H3 F3 W0 plants as above
Dark brown D4–5 H3 F1 W0 *Phragmites*
Dark brown D4 H3 F1 W0–1 Little Alder *Phragmites* Some silt
Silt
Water with *Molinia* roots
Medium brown D3 H3 F2 W0 *Molinia*
Dark brown D3 H4 F2 W0 *Molinia Eriophorum*
Light brown mud *Eriophorum*
Silt
Molinia, Scirpus or *Eriophorum* peat
Phragmites peat
Brushwood peat
Angular gravel
Silt

STRATIGRAPHY OF PEAT AT BORINGS *O, P, Q, R* ALONG LINE *OC*

(*O* is the intersection of *AB* and *CD*.)

Fig. 4.

The whole zone is deeply intersected by wide and narrow channels, which intermingle and form the headwaters of the two streams, the Afon Brefi and the Pysgotwr Fawr. During periods of heavy rain, the channels are the paths of rapid torrents of water, which carry away in suspension comparatively large quantities of peat. The streams are continually widening and deepening their channels as well as cutting back, so that, when followed upstream, the numerous tributaries of the south-eastern and north-western systems cannot be distinguished. It appears that the network of channels towards the head of both streams have coalesced one with the other. This peat moor, which was formerly the gathering ground of both streams, is thus now divided into large hummocks.

In dry periods, cracks appear in the peat of the bare depressions. These cracks have played their part in the formation of the erosion complex and account for the relatively rapid disappearance of surface water, even after heavy rains.

The greatest amount of erosion has taken place at the south-eastern, west and north-western parts of this zone, so that three regions can be distinguished within the erosion complex itself:

(1) The south-eastern, drier, greatly eroded area, running east and south-east from the transect line *K* (Fig. 1).

(2) The central, wetter, less eroded area, between lines *K* and *M* (Fig. 1).

(3) The western, drier, greatly eroded area, from line *M* to the west (Fig. 1).

There is no sharp line of demarcation between the three, but the differences can be correlated with the history of the Afon Brefi and the Pysgotwr Fawr. A certain amount of erosion is still taking place. The fact that these streams have not reached their base level is manifested by the cutting back of both streams into the watershed. The central region, that is, the one in the region of the watershed, is the last part to have experienced erosion by the two stream systems. Regions 1 and 3 possess quite well-defined stream beds, in which run the main streams and main tributaries of the Afon Brefi and Pysgotwr Fawr, respectively.

Key to Fig. 4

Humification table

H 1. Quite unhumified peat; on squeezing, only clear colourless water runs out.
H 2. Almost completely unhumified peat; on squeezing, clear and pale brown-yellow water runs out.
H 3. Very little humified peat; water which is definitely turbid and brown runs out, but no peat comes out between the fingers and the residue is not porridgy.
H 4. Little humified peat; strongly turbid water squeezed out but no peat substance; the residue somewhat porridgy.
H 5. Rather humified: plant structures a little obscured; strongly turbid brown water squeezes out together with some peat; the residue very porridgy.
H 6. Rather strongly humified: plant structures not clear; about one-third of the peat squeezes out of hand; the residue very porridgy but with clearer plant structure than in the unsqueezed peat.
H 7. Strongly humified peat: plant structure fairly recognizable; on squeezing, about half the peat escapes.
H 8. Very strongly humified peat with very obscure plant structure; about two-thirds of the peat squeezes through the fingers leaving only a residue of root fibres, wood fragments, etc.
H 9. Almost fully humified peat almost without recognizable plant remains; almost all the sample squeezes out of the hand.
H 10. Fully humified peat: no plant structure; all the sample squeezes out of the hand.

Woodiness

W 0. Lacking.
W 1. Present in small amount.
W 2. Abundant.
W 3. Making up most of the sample.

Wetness

D 1. Air-dry.
D 2. Damp.
D 3. Average wetness.
D 4. Very wet.
D 5. Water with suspended material.

Amount of fibre

F 0. Lacking.
F 1. Present in small amount.
F 2. Abundant.
F 3. Making up most of the sample.

At the south-eastern end of the erosion complex is a deeply eroded drainage channel, forming the upper reaches of the Pysgotwr Fawr. Here erosion has caused the formation of miniature gorges, some 5 m. wide, and the channels anastomose considerably. During periods of heavy rain the water in the channels flows swiftly, in times of drought the channel beds contain little or no water. Under the latter conditions, the peat dries at the sides of the channels and easily crumbles, the process of drying having been accelerated, undoubtedly, by wind action. As a result, the peat dust is removed by the wind, exposing the root systems of the plants, chiefly of *Calluna vulgaris*. Consequently, the excessive drying results in numerous dying *Calluna* tussocks which are a feature of the sides of the hummocks at this south-eastern end. On such tussocks, *Cladonia sylvatica* and *Rhacomitrium lanuginosum* form the dominant elements of the plant society.

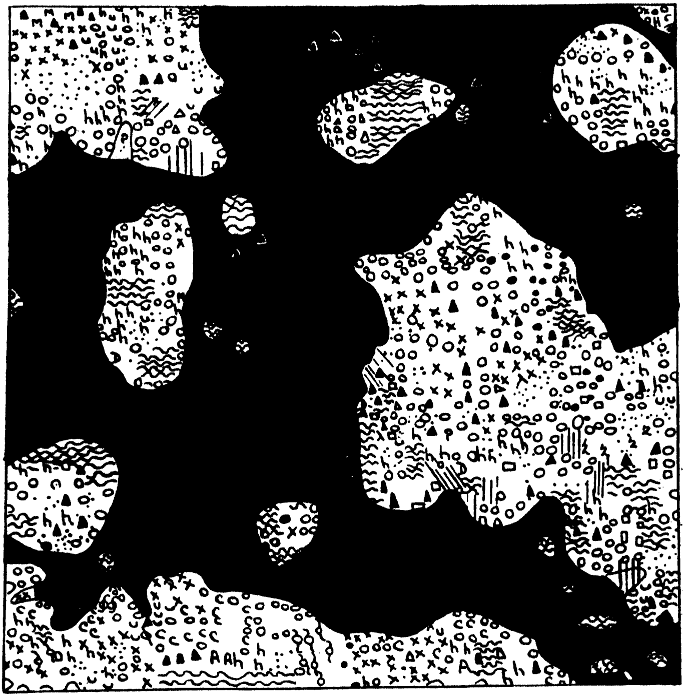


Fig. 5. One metre quadrat in the erosion complex.

Key to Figs. 5, 6 and 7

Andromeda polifolia	A	Drosera rotundifolia	D	Rhacomitrium lanuginosum	X
Bare peat	■	Erica tetralix	⁖	Rhynchospora alba	R
Calluna vulgaris	°o°	Eriophorum angustifolium	▲	Scirpus caespitosus	≋
Campylopus flexuosus	f	E. vaginatum	△	Sphagnum cuspidatum	IIII
Carduus palustris	?	Hylocomium squarrosum	▩	S. papillosum	\\\\
Cladonia sylvatica	⁛	Hypnum schreberi	h	S. plumulosum	§
C. uncialis	u	Molinia caerulea	M	S. tenellum	≡≡≡
Dicranum majus	□ or J	Narthecium ossifragum	N	Viola palustris	V
D. scoparium	Di	Potentilla erecta	E		

In this south-eastern part of the erosion complex, the depressions are, in the main, dry and bare, except for solitary plants of *Eriophorum angustifolium* dotted about at infrequent intervals. *Sphagnum cuspidatum* is rare, and is found only in the wetter parts near the channels. Its absence from the depressions is a conspicuous feature, and it appears to be present in the wetter pool areas only after *Eriophorum angustifolium* has begun colonization. On the other hand, in channels where there is little, if any, flow of water, there is a considerable amount of *E. angustifolium*. These plants cause the silting up of the channel beds, and much silt is seen on the upstream side of the small masses of *E. angustifolium*.

The drier parts of this south-eastern area have numerous tussocks of *Campylopus flexuosa* on the hummocks, while in the depressions between lines *I* and *J* of the grid (Fig. 1) are many small tussocks of *Polytrichum commune*, which are dying out.

The dry area to the west, that is, the area west of the line *M* of the grid (Fig. 1), is similar to the corresponding region at the south-eastern end. Indeed, the vegetation throughout the whole of the erosion complex is very uniform, and the greatest variations in the character of the zone are concerned with the ratio depressions/hummocks. The greatest amount of erosion has taken place in this western area, and two-thirds or more of the total surface area consists of large bare depressions. The hummocks are mostly under 1 m. in diameter, and some are a metre or more in height. The area has the appearance of a peat 'desert' with 'zeugens' formed as a result of wind erosion.

After the isolation of the hummocks, the roots of *Calluna* and other plants are exposed by subsequent wind action. The drainage channels in this region are, for the most part, deep in the peat, but one wide shallow channel occurs, although its presence is much more evident after flooding has taken place.

The hummocks left in the meshes of the network of channels are drained on all sides. As in other parts of the erosion complex, *Calluna vulgaris* is the dominant plant, but the increasing dryness is indicated by the appearance of *Vaccinium myrtillus* on the hummocks. *Nardus stricta* has also been found in this region. It is only in this much-eroded western half of the erosion complex that *Vaccinium myrtillus* is recorded and locally it is very frequent.

The wettest parts of the erosion complex occur in the central region between lines *K* and *M* (Fig. 1), a part which represents an earlier stage in the cycle of erosion which is in progress on the bog. It is here that the characteristic associations are best seen. The erosion complex appears to be a Callunetum which, as will be seen later, has probably been derived from a Scirpetum on account of the gradual desiccation of the peat, subsequent to the action of the eroding agents. The hummocky nature of the surface is a feature of the whole zone, but in this central region many of the hummocks are large and the pools occupy only from one-third to one-half of the total area (Pl. 1, phot. 1).

On the hummocks, *Calluna vulgaris* is the dominant plant, but *Scirpus caespitosus* is abundant often over large areas. With the *Calluna* are associated *Cladonia* spp., chiefly *sylvatica*, while large tussocks of *Rhacomitrium lanuginosum* frequently occur. The *Rhacomitrium* is found mainly at the edges of the hummocks, due to the desiccation caused by the cutting away of the sides and their subsequent erosion.

Between the hummocks are the drainage channels and depressions. It is in this central region that the channels of both the Afon Brefi and the Pysgotwr Fawr drainage systems intermingle, and coalesce. The main tributaries have cut relatively deep, wide channels, but the whole area is intersected by numerous small, shallower channels.

In the wet depressions, *Sphagnum cuspidatum* is rare. It occurs in these pool areas only after *Eriophorum angustifolium* has begun the recolonization. Another pioneer of bog-pool areas which is seen in abundance on the raised bog at Tregaron, is *Rhyncospora alba*. On Blaen Brefi, however, the latter plant is rare and very local in its distribution. It occurs in greatest abundance at one point along line *K* (Fig. 1) in the transition zone between the erosion complex and the Scirpetum.

Drosera rotundifolia, a common occupant of the pool areas on many bogs, is also only of rare occurrence on Blaen Brefi, a few young green plants having been recorded in the wetter parts of the erosion complex (Fig. 5).

An attempt was made to ascertain whether the *Rhyncospora alba* was increasing. For this purpose, recordings were made on a 2 m. quadrat in an area in which *R. alba* occurred in association with *Eriophorum angustifolium*, *E. vaginatum*, *Scirpus caespitosus*, and *Sphagnum* spp. The results showed no appreciable difference in the amount of *Rhyncospora* at the end of 18 months. On 11 February 1939, it was found that the old inflorescence axes had disappeared, and only a few bulbils were visible in the quadrat. This is in contradistinction to the observations on Tregaron where the old axes persisted.

It is evident throughout the erosion complex that in the attempt to recolonize the bare areas, *Eriophorum angustifolium* plays the primary part, such pioneers as *Sphagnum cuspidatum* being rare, and appearing in small patches, only after the *Eriophorum* has begun colonization.

It is significant that *E. vaginatum* only occurs infrequently in the erosion complex. *E. angustifolium* is primarily a more hydrophytic species than *E. vaginatum*, and is much more resistant to such conditions as are obtained at Blaen Brefi, where wind action may result in the destruction of projecting hummocks of *Eriophorum*.

Some fifteen months' observations on Blaen Brefi led to the opinion that parts of the erosion complex had begun to be recolonized by *E. angustifolium*. This recolonization, where the drainage channels are wider and shallow, has proceeded to such an extent that throughout the zone considerable areas of *E. angustifolium* occur in close association. In the wet central region, the various stages in this process are best seen. At the western end, the large areas which are bare of *Eriophorum* can be correlated with the drying and eroding effect of the wind.

An attempt was made to ascertain the extent to which increased colonization by *E. angustifolium* was occurring. A number of 1 m. quadrats were made in the channels and in the depressions. The plants were recorded before the winter frosts, so that subsequent frost action was taken into account, and the quadrats were observed at intervals.

At the end of a year, it was evident that in all cases *E. angustifolium* was a primary colonizer in this region, and that in all the areas examined the plants were increasing considerably. This increase is greatly influenced in autumn and winter by the fact that the erect axes of some plants are found to be damaged at the base, while other plants are nipped off and lie flat on the peat. The same phenomenon is seen in *Rhyncospora*, and is attributed to attack by birds, mainly curlews, who pull up either whole pieces of rhizome, or peck off the white succulent shoot just below the ground level. In this way, large areas are destroyed, and recolonization necessitated.

Thus, while in some areas erosion is very active, the process is checked by *Eriophorum angustifolium*. Wind and water, however, are not the only agents of erosion at Blaen Brefi. Frost, ice and snow all play their part. During the winter, the area is subject to heavy falls of snow, and to severe frosts, ice being formed even on the swiftly running water in the main channels.

It is evident that frost separates the surface particles of peat in the drainage channels. The subsequent thaw results in a levelling of the surface of the bases of the channels and the peat particles become finely separated, the whole giving the appearance of a fine scum. Under these conditions, subsequent water erosion has its maximum effect. The waterlogging resulting from the thaw after the frost causes the small hummocks to become very soft and easily overturned.

The following plants are found in the erosion complex:

Calluna vulgaris	d.
Rhacomitrium lanuginosum	a.
Cladonia sylvatica	c.
C. uncialis	r.l.
C. coccifera	f.
Polytrichum commune	r.l.
Scirpus caespitosus	a.
Eriophorum angustifolium	a.
E. vaginatum	r.l.
Hypnum schreberi	c.
Molinia caerulea	f.
Erica tetralix	r.
Drosera rotundifolia	r.
Andromeda polifolia	r.l.
Vaccinium myrtillus	r.
Rhyncospora alba	r.l.
Dicranum majus	f.
Campylopus flexuosus	f.
Sphagnum cuspidatum	r.
S. plumulosum	f.
S. tenellum	r.l.
Nardus stricta	r.
Lycopodium selago	r.

Scirpetum

To the north and north-east, the erosion complex is succeeded by a Scirpetum, a zone which is very broad in the centre but narrows considerably to the north-west and south-east (Fig. 1 and Pl. 1, phots. 1, 2). A smaller area of Scirpetum occurs both to the west and south-west, and to the south-east of the erosion complex.

The northern Scirpetum occupies the largest area of the bog, and is a wet but firm zone whose uniformity is broken locally by Molinietum. In this Scirpetum the watershed is clearly seen to be approximately along grid line J (Fig. 1) from which the land slopes gently to the south-east on the one side and to the north-east in a long gentle uniform slope on the other.

Throughout the zone the plants of the association are well distributed and the following occur:

Scirpus caespitosus	d.
Molinia caerulea	l.a.
Eriophorum angustifolium	a.
Erica tetralix	f.
Calluna vulgaris	r.
Narthecium ossifragum	l.a.
Potentilla erecta	l.a.*
Dicranum majus	f.
D. scoparium	r.
Cladonia sylvatica	r.
Hypnum schreberi	f.
Polytrichum commune	r.
Campylopus flexuosus	l.f.
Sphagnum cuspidatum	l.a.
S. papillosum	f.
S. plumulosum	f.
Polygala vulgaris	l.*

* In wetter parts.

The ground is much less broken than in the erosion complex, and the large deep depressions of that area are replaced by long, narrow, shallow, linked pools, with much *Sphagnum cuspidatum* and *Eriophorum angustifolium* (Fig. 6). The absence of *Calluna vulgaris*, except at the southern margin of the zone, serves to delimit it rather sharply from the adjacent erosion complex. Its northern limits, where it merges into the Molinietum, however, are less definite.

On the northern edge of the Scirpetum to the west, a large drainage channel has caused considerable erosion. In this region there is much bare peat on the sides of the channel, and large tussocks of *Molinia* stand high above the general ground level. Apart from this, the zone is not well drained, and much of the peat is waterlogged, a fact which probably contributed to the occurrence of a large amount of *Sphagnum cuspidatum*.

Scirpus caespitosus is the dominant plant of the association, but the local wet depressions are dominated by *Eriophorum angustifolium*.

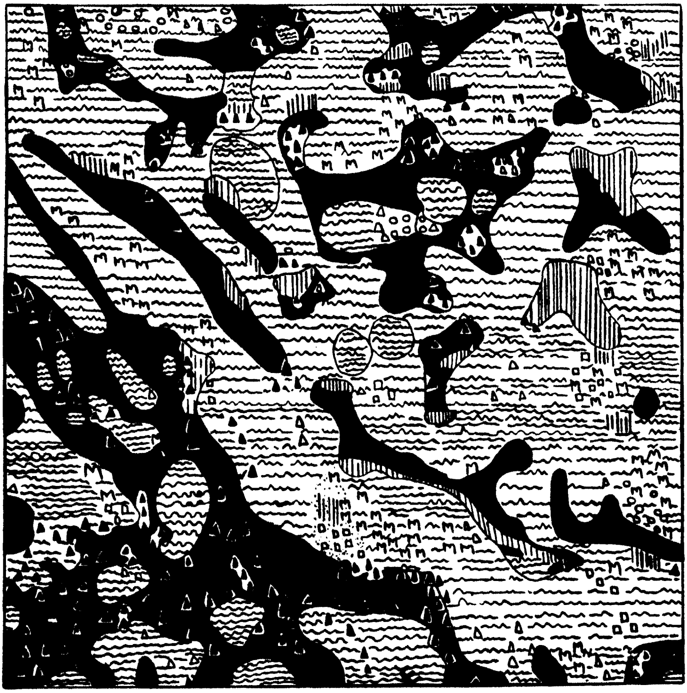


Fig. 6. One metre quadrat in the Scirpetum.

The *Scirpus* is of a tufted nature and each tuft is made up of a number of small 'units', each consisting of one, two or three small erect shoots, while others consist of one or more of these units, united together by a horizontal rhizome.

The smaller areas of Scirpetum on the western and southern sides of the erosion complex are topographically and floristically similar to the northern Scirpetum, and a characteristic feature of all the areas is that they are regions of little slope. Floristically they are poor, the species of flowering plants being very restricted in number.

The Scirpetum is an especially interesting area of the bog, and its relation to the adjacent zones will be considered later.

Molinietum

On the hills around the bog proper is *Molinia* pasture, associated with thin peaty soil, some 2 ft. deep. On the bog itself, large patches of Molinietum abut on the Scirpetum, though they are broken in places by considerable areas of Juncetum. The transition from Scirpetum to Molinietum is a very gradual one, large areas of the bog consisting of Scirpetum-Molinietum, where *Scirpus caespitosus* and *Molinia caerulea* are co-dominant.

Throughout the true Molinietum the ground is very broken, and the *Molinia* occurs in tussocks of varying size. Associated in the tussocks of the dominant plant is abundant *Polytrichum commune* and *Sphagnum papillosum*, while *Hypnum schreberi* creeps over the surface (Fig. 7).

The pools between the tussocks are colonized by *Sphagnum cuspidatum*. The Molinietum occupies the drier, better drained areas of the bog. The pools are very indistinct; there is considerably less *Polytrichum commune* than in the *Juncus* zone, and *Erica tetralix* is common.

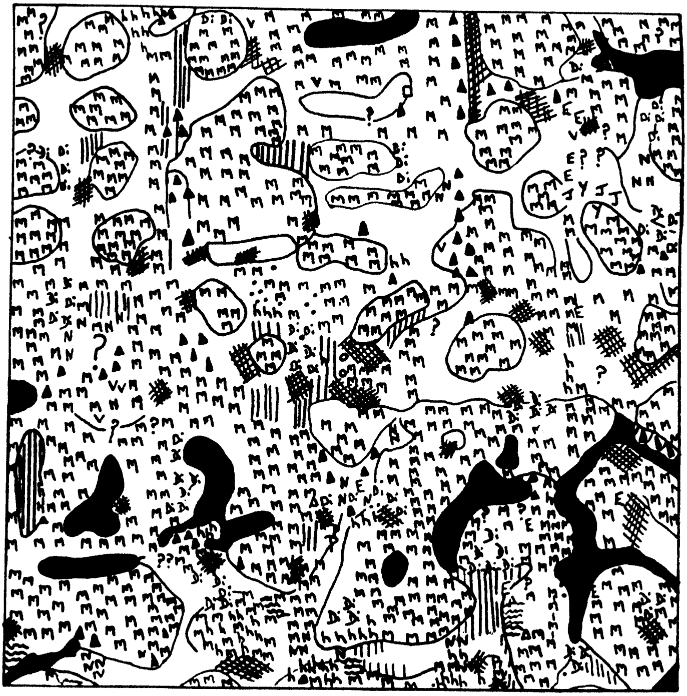


Fig. 7. One metre quadrat in the Molinietum.

The Molinietum occurring near the Juncetum contains some species characteristic of the latter zone.

The plant list is as follows:

Molinia caerulea	d.	Potentilla erecta	f.
Scirpus caespitosus	c.	Galium palustre	f.
Eriophorum angustifolium	c.	Polygala vulgaris	r.
Polytrichum commune	a.	Juncus effusus L.	f.
Hypnum schreberi	f.	Potentilla palustris	r.
Calluna vulgaris	l.f.	Sphagnum cuspidatum	a.
Erica tetralix	f.	S. plumulosum	f.
Vaccinium myrtillus	c.	S. papillosum	f.

Juncetum

There are large areas of Juncetum to the north-west, and also to the south of, and abutting on, the erosion complex. In the north-west and north, large areas of Juncetum occur within the Molinietum, while in the south-east is a considerable area of Juncetum-Molinietum, which merges into the *Molinia* pasture.

All these are regions of wet soil which in the northern zone marks the sources of some of the small streams which eventually flow into the Afon Brefi. In the issuing water, such plants as *Potamogeton natans* and *Galium palustre* are found. The *Juncus effusus* L. occurs in tussocks in association with *Polytrichum commune*, and thus the ground is very broken. In the wet areas between the tussocks, *Sphagnum cuspidatum* is abundant.

The Juncetum proper is a much better drained area than the Scirpetum (Pl. 1, phot. 1), and a significant feature of the northern and south-eastern zones is that both occur in areas of increased slope at the foot of the hills. *Juncus effusus* L. also forms narrow zones along the banks of the Afon Brefi and some of its tributaries. All these facts are in accordance with the observations made on other peat areas, which will be discussed later.

Near the stream which follows the line *M* in the Juncetum (Fig. 1) is a society of stagnant hollows. These are large pools where the water is stagnant, and they present the appearance of miniature lakes, with submerged carpets of *Sphagnum cuspidatum*. The species present here include *Polytrichum commune*, *Hypnum schreberi*, *Hylocomium squarrosum*, *Viola palustris* and *Hydrocotyle vulgaris*.

South of the erosion complex is a small patch of Juncetum, but it forms part of the large Sphagneto-Juncetum which skirts the erosion complex on its southern and western side (Fig. 1). This Sphagneto-Juncetum is very soft, and it appears that the carpet of *Sphagnum cuspidatum* and its associated plants 'floats' on a very wet substratum. This Sphagneto-Juncetum probably indicates the site of a former stream bed, which possessed a slow-moving stream, and/or was subject to extensive floods. This point will be discussed later, after a consideration of the boring, levelling and stratigraphy of the region.

The following plants occur in the Juncetum:

Juncus effusus L.	d.	Molinia caerulea	f.
J. sylvaticus	l.f.	Viola palustris	l.f.
J. bulbosus	l.f.	Hypnum schreberi	c.
Polytrichum commune	a.	Deschampsia flexuosa	r.
Galium palustre	f.	Sphagnum cuspidatum	a.
Potentilla erecta	f.	Hylocomium squarrosum	c.
Carduus palustris	o.		

In the Sphagneto-Juncetum, *Sphagnum cuspidatum* is the dominant plant, forming very considerable carpets on which are found *Potentilla palustris*, abundant *Potamogeton natans* and *Viola palustris*, the last more frequent than in the Juncetum proper.

BORING, LEVELLING AND STRATIGRAPHY

Two series of levels were taken across the bog (see Fig. 1, lines *AB* and *CD*). The line *AB* crosses the watershed, while *CD* passes over the two areas of Scirpetum as well as part of the erosion complex and the wet Sphagneto-Juncetum in the west. A series of borings showed that the peat is underlain by boulder clay, the configuration of which is followed in general by the present surface of the bog. In some parts, however, local topographical variations in the boulder-clay surface have had their influence on the depth of peat.

A study of the diagram along the line *AB* (Fig. 2) shows that the greater part of the area is a catchment for the westward-flowing Afon Brefi, the top of the watershed occurring far to the east of the bog. There is a general slope to the west, the bog surface at its highest point being approximately 12 m. above datum, the latter being approximately 410 m. (1350 ft. O.D.).

It is seen that the line begins in the Molinietum on the north-west where the peat is about 3 m. deep and falls to the valley of the Afon Brefi, which runs in a deeply incised channel at the base of which the peat is cut away to a depth of 0·6 m. From the river, the general surface rises gently for a distance of 600 m. to the top of the watershed, and the line passes successively through the much-eroded ground of the erosion complex, in which is a small area of Molinietum-Scirpetum, to the large area of Scirpetum which is at present the most actively growing region of the bog. An examination of this section of the diagram reveals the fact that a rise in the surface of the underlying boulder clay is accompanied by a thinning out in the peat, so that two areas where the peat reaches a depth of almost 4 m. are separated by a region where the accumulation is shallower. The south-eastern end of the line cuts the Pysgotwr Fawr at right angles, and in this region the peat is seen to have been eroded at two points where streams are encountered. The extreme end of the line shows a slight rise in level, which continues up the hillside to the *Molinia* pasture.

The line *CD* (Fig. 3) passing approximately from west to east, commences at the thin peat of the hillside and soon crosses the small area of Scirpetum. It passes subsequently across the Sphagneto-Juncetum and to the eastward crosses both the valley of the Afon Brefi and the erosion complex, and then passes across the deep peat laid down in a slight depression on the valley floor near the edge of the erosion complex. It continues across the relatively deep peat of the main Scirpetum. At the extreme easterly margin of the section, the peat of the Scirpetum is thinning out as the *Molinia* pasture of the adjacent hillside is approached.

It will be seen, however, on comparing sections *AB* and *CD* that three shallow depressions occur in the configuration of the boulder-clay surface, one in the region of the present watershed, one to the westward in the deepest part of which boring *O* has been made, and one still farther to the west which coincides with the site of the present Sphagneto-Juncetum.

More detailed stratigraphical examination of the peat has been made at a few points along *OC*, *O* being the point of intersection of *AB* and *CD*, and being also in one of the regions of deep peat. It will be seen from Fig. 4 that a layer of silt occurs immediately above the boulder clay, followed by about 48 cm. of wet, light brown *Phragmites* peat, which contains no brushwood. This is succeeded by 160 cm. of *Phragmites* brushwood peat, in which both birch and alder are present. This peat is in the main darker brown than the *Phragmites* peat, and is progressively less humified in its upper layers. In places in the erosion complex, this brushwood peat is exposed.

In view of the interesting topography south-westward from *O*, other borings were taken at points *P*, *Q*, and *R* along the line *OC* (Figs. 3, 4). Point *P* occurs in the Sphagneto-Juncetum, and it will be seen that a layer of silt and gravel overlies the boulder clay, followed by a band about 10 cm. wide, of angular hill-wash gravel. Above this a small zone of *Phragmites* peat is overlain by a band some 20 cm. wide, of dark brown birch-alder-brushwood peat. This is succeeded by 16 cm. of dark brown *Phragmites* peat, which passes over into a wide band of *Eriophorum angustifolium* peat, with some *Phragmites*. This is the only boring in which *Eriophorum angustifolium* is associated with the *Phragmites*. It is of interest inasmuch as this area appears to have been the site of an old watercourse, the path of which may still be seen in the present Sphagneto-Juncetum, although the depression in which it arose is now filled up. *Eriophorum angustifolium* is more commonly associated with acid-bog conditions, but it is not extremely oxyphilous, and has been recorded locally in the East Anglian Fens (Tansley, 1939, p. 664). This *Eriophorum-Phragmites* peat is some 88 cm. in depth, and is succeeded by 30 cm. of dark brown *Eriophorum* peat. The top 98 cm. is occupied by water containing suspended *Sphagnum* and *Juncus*, both very little humified.

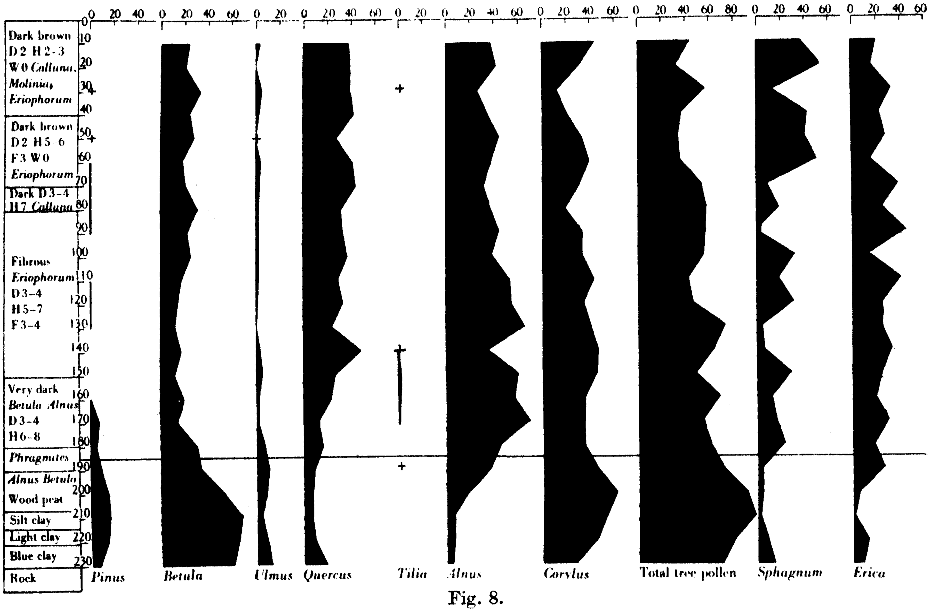


Fig. 8.

The point *Q* is farther to the west at the Scirpetum margin of the Sphagneto-Juncetum. At the base the silt is succeeded by 53 cm. of dark brown *Phragmites* peat, containing a little alder throughout, and also some silt in the lower layers. Above this lies 36 cm. of dark brown *Phragmites* peat, which is slightly wetter than the previous layer, and in which brushwood is absent. The *Phragmites* peat is followed by 142 cm. of peat containing the remains of *Molinia*, *Scirpus*, *Carex* and *Eriophorum*, the lower layers of which are darker in colour than the upper 30 cm. In the uppermost 32 cm. the bore filled with water.

Point *R* occurred at the base of the hill where the peat was considerably thinner. The basal silt was followed by 8 cm. of light brown muddy peat, containing remains of *E. angustifolium*. Above this occurred 88 cm. of *Molinia* peat. The lowest 46 cm. of this *Molinia* peat contained much *Eriophorum* and is dark brown in colour. The succeeding 32 cm. consisted of less humified, almost pure *Molinia* peat of medium brown colour, while in the top 10 cm. the borer was filled with water containing *Molinia* roots.

Borings on the main Scirpetum on the eastern side of *O* showed a definite wood peat at the base of the core, lying directly on the boulder clay. It will be suggested later that the surface ecology of Blaen Brefi is comparable with that of a bog near the Teifi pools, Cardiganshire. In this latter area, J. B. Jones (unpublished) has found that in some places wood remains occur lying directly on the boulder clay, while in others the wood is separated from the boulder clay by a layer up to 50 cm. in depth, of dark, highly humified amorphous peat.

A preliminary investigation of the pollen analysis was made by J. B. Jones (as yet unpublished) (Fig. 8). This shows points of comparison with other bogs in the county. A small amount of *Ulmus*, with small and discontinuous distribution of *Tilia*, compares with the data obtained from Tregaron and Rhos Rhydd. An early *Pinus-Betula* co-dominance gave way subsequently to woodland in which *Alnus* and *Quercus* were co-dominant, with *Betula* and *Ulmus* still present. The woods appear to have been replaced ultimately by vegetation in which *Eriophorum angustifolium* was dominant.

Where the total depth of peat was 230 cm. the change from a *Pinus-Betula* co-dominance to *Alnus* and *Quercus* took place at about 185 cm. This appears to indicate either the change from Godwin's zone VI to zone VII (Godwin, 1940, p. 374) or alternatively, the basal high *Betula* may have been a local effect in the subboreal period and the upper part of the diagram may then belong entirely to zone VIII (Godwin, 1940, p. 376). In view of the fact, however, that there is a decrease in the *Corylus* below the 185 cm. line, and a sharp rise in the *Betula* above, it seems more likely that the line represents the change from zone VI to zone VII.

DISCUSSION

An attempt has been made to determine the interrelationships of the associations on Blaen Brefi. The bog, occupying as it does a declivity between two hills, is an example of a particular bog type found in Cardiganshire, in which the centre is occupied by an erosion complex from which river systems drain in two directions.

Except for the narrow Sphagneto-Juncetum zone, the erosion complex forms an uninterrupted 'core' at Blaen Brefi. It is greatly intersected by the channels of the two river systems, the Afon Brefi and Pysgotwr Fawr, and these channels anastomose and coalesce considerably. The erosion complex is in the main a Callunetum which has developed on the drier peat of the area. On all except its southern margin it is adjacent to the Scirpetum, which latter is associated with little slope and deep peat. Owing to the lack of drainage channels, the Scirpetum is saturated at most times of the year. The southern margin of the erosion complex is but a short distance from the base of the hills which are covered with *Molinia* pasture, associated with thinner and better drained peat.

Like the Scirpetum, the Callunetum is associated with deep peat, and thus it appears to have been developed from some other community which has been superseded by *Calluna vulgaris* as a result of drying. The well-developed drainage systems leading out into the Afon Brefi to the north and into the Pysgotwr Fawr to the south-east, account for the draining of the area, and the resultant drier peat. It would appear therefore that there has been a succession from Scirpetum to Callunetum as a result of the drying of the peat which has been effected by the cutting back of the two streams into the watershed with a consequent lowering of the water-level.

The position of the watershed and the occurrence of the erosion complex on deep peat is shown in the section line *AB* (Fig. 2). This diagram supports the theory that the dominance of *C. vulgaris* is due to the drying out of the peat as a result of more extensive drainage by the two river systems. In addition, it is significant that the erosion complex is for the most part surrounded by Scirpetum.

A little *Vaccinium myrtillus* has been recorded at the western edge of the erosion complex, and a few plants are found at the drier south-eastern end. However, on an exposed high-lying peat land, such as Blaen Brefi, which is above the tree limit, the *Calluna* probably represents the climatic climax. This view is supported by the fact that there is no burning and very little sheep grazing, either of which might have been regarded as tending to prevent the development of a *Vaccinium* climax vegetation.

Within the Callunetum itself, *Calluna vulgaris* is not overwhelmingly dominant, *Scirpus caespitosus* is abundant, and sometimes even co-dominant. Where the erosion complex abuts laterally on the Scirpetum, erosion continues, the streams progressively cutting farther up the slopes. Marginally, a transition zone occurs in which some *Erica tetralix*, a little *Cladonia*, and a small amount of *Calluna* have begun to make their appearance. It suggests that the streams cut their way back into the Scirpetum and drain the pools, so that the consequent drying causes the commencement of a vegetation change, which reaches its maximum in the centre of the erosion complex.

A comparison has been made with other bogs in the neighbourhood, and more especially with a small mountain bog near the Teifi pools. This bog occurs at a height of 440 m. (1450 ft.), and lies between two parallel hills. The area is drained by two streams which run out in opposite directions, the watershed being near the centre of the bog. The general form of the bog is very similar to Blaen Brefi, although it covers a much smaller area. The vegetation also is essentially similar.

At this small bog, the two streams are actively cutting back, and each stream drains an area of erosion complex, dominated by *Calluna vulgaris*. The process of cutting back, however, is incomplete, and instead of the two systems having coalesced, a 'bridge' of Scirpetum remains between the two Callunetum areas. The headwaters of both streams continue to incise channels in this small area of Scirpetum. By following the vegetational changes down both valleys, it is evident that the present vegetation of the erosion complex has been formed subsequent to, and as a result of, the process of erosion. When this process has begun, the uneroded areas become drier and new species make their appearance. The stages may be traced in the transition from the Scirpetum to well-developed erosion complex. One of the first changes is the appearance of *Erica tetralix*, which is followed later by *Cladonia* species, together with *Calluna vulgaris*, and *Rhacomitrium lanuginosum*. The three latter form the vegetation of the dry summits of the tussocks, and *Eriophorum angustifolium* is attempting a secondary colonization of the pool areas.

Thus, all the evidence suggests that the erosion complex at Blaen Brefi has been developed from the Scirpetum as a result of the cutting back of the headwaters of the two streams. The early stages in the vegetational succession which has been caused by this phenomenon are at present being repeated where the margins of the erosion complex abut on the Scirpetum and similar conditions of drainage result.

Though the cutting back of the streams has been the primary factor in the development of the erosion complex from the Scirpetum the many other agents of erosion have played prominent parts in the formation of some of the characteristic features of the area.

Water erosion results in the exposure of bare peat-faces along the sides of the channels. Subsequent wind action results in the drying of the peat and the removal of the fine particles. Such erosion is a characteristic of many of the high mountain bogs in Cardiganshire. Throughout the erosion complex at Blaen Brefi, and particularly at the drier western and south-eastern ends, numerous small, isolated tussocks occur. In addition to causing the roots of the plants to be exposed, wind action results in the formation of a 'waist' in each tussock, above which is a large head of vegetation. At the top of the tussock the root systems of the present vegetation tend to prevent erosion, but below, the peat easily crumbles after drying. Continued wind action leads to the collapse of the tussock. This has taken place at the western and south-eastern ends of the complex and has resulted in the formation of large areas of bare peat. These areas are, for the greater part of the year, dry and much cracked. Even during the flood season, the numerous drainage channels and the cracks in the peat allow of a comparatively rapid disappearance of the water. Under such conditions, wind erosion is very active; the dry surface layers of peat are easily removed, and any tussock which stands above the general surface level is soon destroyed.

The dryness, too, results in a conspicuous absence of any quantity of *Eriophorum angustifolium* in the depressions, a feature in which the two drier areas differ markedly from the central wetter region where this plant is attempting to colonize the pool areas.

As already explained, frost, ice and snow all play their part in the formation of the erosion complex. The spring thaw of the winter ice and snow results in a levelling of the surface, partly by causing the peat particles to become finely divided, and partly because the thaw results in a waterlogging which causes the peat hags to become very soft and easily overturned.

The effect of these destructive forces has resulted in the partial colonization of the wetter pool areas and drainage channels by *E. angustifolium*. In all the areas examined, there has been a considerable increase in the extent of this colonization, but its effect would be much more marked were it not for the destructive work of birds. Over large pool areas where there has been a sparse cover of *E. angustifolium*, all the plants have been destroyed. In winter when food is scarce, curlews pull up the shoots of the *Eriophorum* and peck the white succulent portion at the base.

The Scirpetum is an interesting area, inasmuch as it covered formerly the greater part of Blaen Brefi. With the continued cutting back of the streams it is developing into Callunetum, where it abuts on the erosion complex. The soil is thick peat, which is thoroughly saturated with water for the greater part of the year. *Scirpus caespitosus* forms large separate tufts between which occur the soft wet peat of the pool areas. This Scirpetum is still actively forming peat. The pools away from the drainage channels are being colonized by *Sphagnum cuspidatum* and *Eriophorum angustifolium*. Later *Scirpus caespitosus* establishes itself together with some *Erica tetralix*. Extensive erosion, however, has resulted in a process of degeneration, which is continuing and is causing an encroachment of the Callunetum upon the true Scirpetum.

The Molinietum is one of the 'drier' communities in this wet peat area, colonizing in abundance the higher, better aerated ground towards the hill slopes. *Molinia caerulea* also colonizes peat formed by other plants, and is found in large quantities in the drier parts of the erosion complex and the Scirpetum. It occurs in the Scirpetum, especially near the larger drainage channels. Elsewhere it appears to be on the margins around the main peat area, and its occurrence here as well as on the surrounding hills suggests that its prevalence is the result of a better supply of bases. The Molinietum is dominated by large tussocks of *Molinia caerulea*, which is associated with the wet peat plants. The

Molinia pasture of the hills forms a peaty sod, varying in thickness from a few inches to 1 ft., which is easily separable from the mineral soil below.

The sources of small streams in the area are characterized by an association of *Juncus effusus* L., which occurs both on the wet spongy banks, and in undrained places. In the Juncetum areas there is much stagnant water containing *Sphagnum cuspidatum.*

SUMMARY

Figyn Blaen Brefi, altitude approximately 1350 ft., lies in a declivity between two hills, and forms the watershed of the Afon Brefi and Pysgotwr Fawr. It is an example of a particular Cardiganshire bog type.

The peat overlies boulder clay, and the headwaters of the two streams have cut back into the watershed until their channels have coalesced. Formerly the vegetation was dominated by *Scirpus caespitosus*, but the lowering of the water table, due to erosion, has caused vegetational changes, so that now a Callunetum forms a continuous band down the centre of the bog.

The bog margin merges into the *Molinia* pasture of the hills, strips of *Juncus effusus* L. occurring in places on the hill slopes.

Preliminary investigation of the peat suggests that Figyn Blaen Brefi developed from *Phragmites* swamps, in depressions in the boulder clay. An early *Pinus-Betula* co-dominance gave way subsequently to woods in which *Alnus* and *Quercus* were co-dominant, with *Betula* and *Ulmus* still present. These woods appear to have been replaced by a vegetation in which *Eriophorum angustifolium* was dominant. Still later, a Scirpetum was developed, parts of which are still actively growing. It is from the Scirpetum that the present erosion complex has been formed. Though the latter is a retrogressive stage, and the vegetation in the drier parts is dominated by *Calluna vulgaris*, in the wetter areas *Eriophorum angustifolium* is attempting recolonization.

Permanent quadrats have been enclosed and marked areas are under observation, in order that the interrelationships of the main vegetational zones may be further elucidated.

This paper represents part of a larger projected scheme of work, which, of necessity has been temporarily postponed. The work has been carried out in the Botany Department of the University College of Wales, Aberystwyth, under the direction of Prof. L. Newton, to whom I am also much indebted for helpful advice and criticism in the preparation of this paper for publication. To Dr H. Godwin I owe much of my interest in this branch of botany, and I am grateful to him for his advice, particularly on the methods and interpretation of peat stratigraphy and analysis. I wish also to express my gratitude to Dr J. B. Jones, Aberystwyth, for allowing me to include the pollen-analysis data, which forms part of his Cardiganshire investigations, as yet unpublished.

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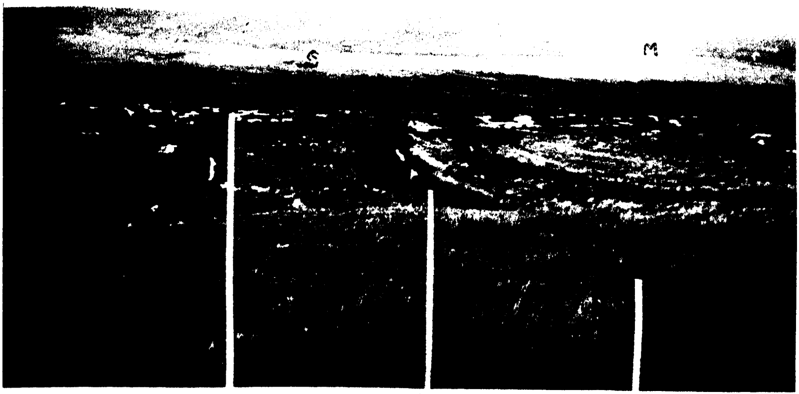


FIG. 1 A. B. C.
General view of Plaen Trefi looking
N.E., showing the zonation of the bog.

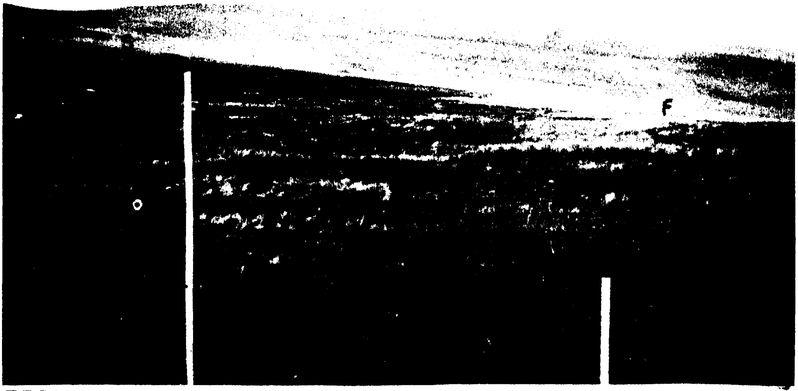


FIG. 2 A. C.
General view looking E.N.E showing
valley of Pysgotwr Fawr.

CADER IDRIS AND CRAIG-Y-BENGLOG

THE STUDY OF THE DISTRIBUTION OF FLORISTICALLY RICH LOCALITIES IN RELATION TO BED-ROCK

By E. PRICE EVANS

(*With Plate* 2 *and two Maps in the Text*)

CONTENTS

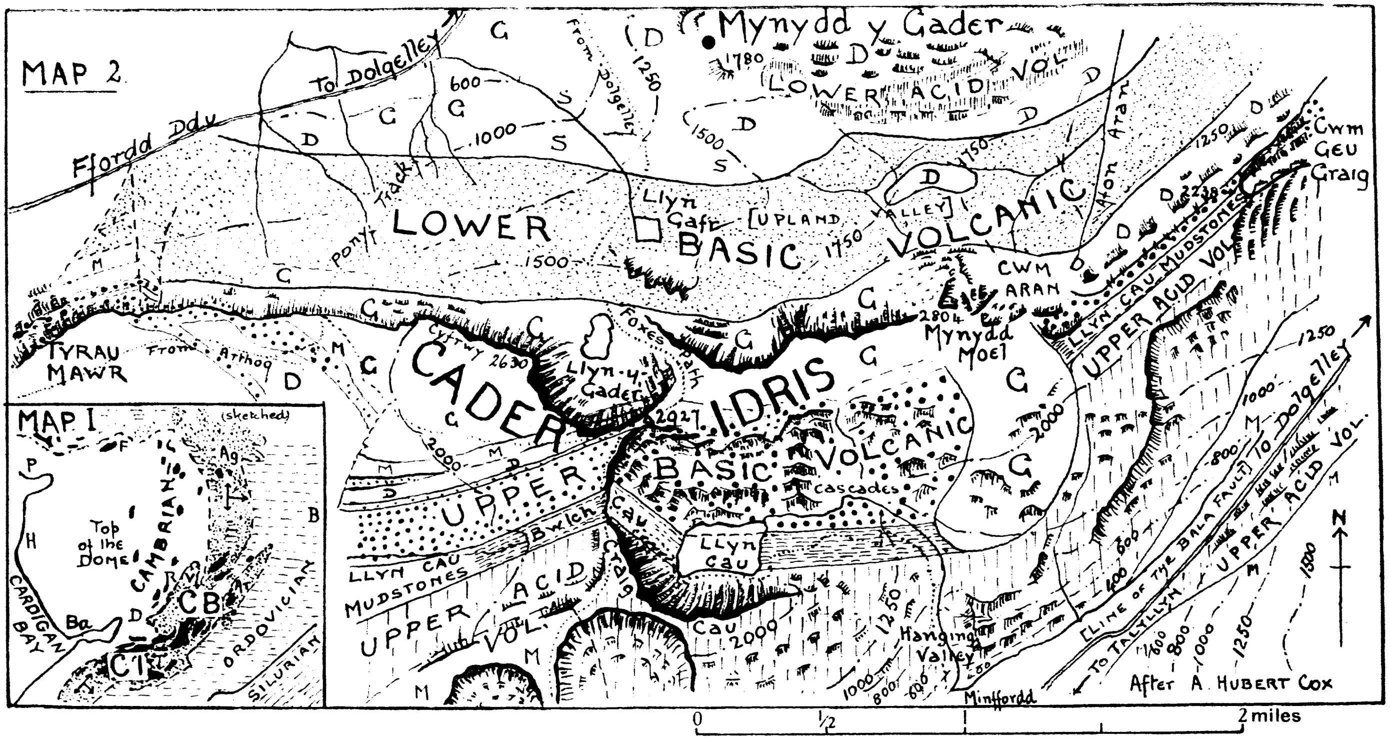
	PAGE
GEOLOGY OF THE AREA	167
FLORISTICALLY RICH LOCALITIES	169
(*a*) Cwm Cau	169
(1) Cascades	170
(2) Craig Cau	170
(*b*) Cwm Geu Graig	170
(1) South-facing slope	171
(2) North-facing slope	171
(*c*) Tyrau Mawr	171
(*d*) Craig-y-Benglog	172
(1) The rock face	172
(2) The upland ashwood	172
(*e*) The Llyn Gafr and Llyn Aran rocks	175
(*f*) The acidic rocks	175
PLANT RECORDS	176
SUGGESTIONS CONCERNING FIELDWORK	177
SUMMARY	178
REFERENCES	179

In a previous paper on the vegetation of Cader Idris (Price Evans, 1932) attention was largely focused on the great (north-facing) escarpment within a selected transect: this paper contains some notes on floristically rich localities outside the transect (one—Craig-y-Benglog—outside the Cader area), on the relation of these localities to the nature of the bed-rock, and a short discussion on fieldwork in the district.

GEOLOGY OF THE AREA

The inset map (Map 1) shows the Harlech Dome of Cambrian rocks with contemporaneous and intrusive igneous rocks on its inner, and sedimentary rocks of Ordovician and Silurian age on its outer flanks (Smith & George, 1935). The igneous rocks (with the flora of parts of which this paper is chiefly concerned) consist of volcanic rocks with intrusives and intercalations of slaty material partly of Cambrian but mostly of Ordovician age. This ‘ring fence of volcanoes’ round the Harlech Dome comprises, as a whole, the highest ground within the area of the map, with peaks rising above the centre of the dome itself. Speaking generally the strike swings round the dome and the strata dip away from it, normally at angles of about 40°, but locally steeper and in places rising even to vertical.

The larger map (2) is a simplified physical and geological map of Cader Idris showing the chief physical features, the four groups of volcanic rocks of the Cader sequence, the main sills of dolerite and granophyre, and some of the sedimentary rocks. The Lower Acid Volcanic group forms the summit of the great dolerite sill of Mynydd-y-Gader and the Lower Basic Volcanic group occupies the floor of the Upland Valley and the slopes under (north of) the great granophyre escarpment: the Upper Basic Volcanic group forms the upper part of the main dip slope and some of the highest points of the escarpment and the Upper Acid Volcanic group comprises the lower parts of the dip slope with, in places, high ‘scarps’—one of them, Craig Cau, surpassing in magnitude any rock face within the area.



Map 1 (inset). CI, Cader Idris; CB, Craig-y-Benglog; RV, Rhobell Fawr; Ar, Aran Mawddwy; Ag, Arenig; D, Dolgelley; Ba, Barmouth; H, Harlech; P, Portmadoc; F, Ffestiniog; B, Bala. ▨ Contemporaneous igneous rocks; ■ intrusive igneous rocks; ⊤ strike-dip.

Map 2. D, dolerite; G, granophyre; S, slates; M, mudstones.

FLORISTICALLY RICH LOCALITIES

In general, it may be said that these localities are on or about the basic volcanic rocks—both upper and lower—the determining factor being the presence of lime in a form (calcite) readily available for plants. Certain physical factors—an abundance of running (preferably dripping) water, the presence of flat ledges and 'pockets' of good soil—are of considerable importance, and when both factors (chemical and physical) are present the flora is rich indeed. There are, however, one or two rich localities where the rocks are only slightly calciferous (if at all) but where the physical conditions mentioned are at their best. These will be considered later on in the paper.

For convenience of description these localities will be treated separately in the following order: Cwm Cau, Cwm Geu Graig, Tyrau Mawr, and Craig-y-Benglog (the latter lying outside the Cader area). Two other rich localities, the Llyn Aran rocks and the Llyn y Gafr rocks (with the pillow-lava band of the Lower Basic) have been dealt with, in more or less detail, in the previous paper; but a few general remarks will be added together with a discussion of the contrast between their flora and that on the great sill of granophyre.

(*a*) *Cwm Cau* (Pl. 2, phot. 2)

This upland valley is one of the most interesting geological and topographical features in the country, and for the grandeur of its scenery and its impressive solitude it is hardly surpassed. Originally a normal river valley (carved out of the relatively soft Llyn Cau mudstones) forming the headwaters of a 'radial' stream which flowed southwards into the Dulas (Corris valley), it was later 'captured' by the transverse stream flowing westwards through Talyllyn. It is to-day a typical glaciated upland valley with corrie-lake (Llyn Cau), roches moutonnées, blocs perchés—the valley hanging about 800 ft. above the Talyllyn valley. The cwm is bounded on its southern and western sides by the enormous 'chimneyed' buttress of Craig Cau, and on its northern side by the rough dip slope of Cader Idris under the summit plateau.

Craig Cau, on the Upper Acid rocks, is relatively sterile, but at its northern end—on or about the 'passage beds' between the acid volcanic rocks and the Llyn Cau mudstones—the flora is particularly rich. These 'passage beds' are ashy slates transitional in position between the mudstones and the volcanic rocks. Judging by the presence here of some calcicole species there is a suspicion that these transitional beds, including the (geologically) upper part of the mudstones, are somewhat calciferous, though the abundance of water, ledges, 'pockets', etc., are probably the determining factors.

Craig Cau (not Craig-y-Cae as it is often written) should not be confused with the dip slope of Cader Idris: what is (locally) known as Craig Cau is the vertical buttress (with chimneys) that rises 330 m. above Llyn Cau. The distinction is important because Craig Cau belongs to the Upper Acid Volcanic group whereas the dip slope belongs to the Upper Basic Volcanic. The dip slope of the Upper Basic rocks is moderately rich in species, especially where there is an abundance of water dripping over calciferous rocks as at the 'Cascades'. On this dip slope, 'one or two dolerite sills appear to be entangled with the pillow-lavas....The rocks have not, however, been separately mapped, owing partly to the difficult nature of the ground, and partly to the difficulty of distinguishing between intrusive and extrusive rocks in the field. The local failing of pillow structure is no certain guide. A vesicular character is also no guide, since the intrusions are usually vesicular towards their margins. Similarly, the texture is not always a safe guide, especially if the intrusion is small' (Cox, 1925). The kind of vegetation, however, is a good guide: the presence of calcicole species points to lavas rather than dolerites. (Even when flowering plants are absent, distinctive cryptogamic species—mosses and lichens—are generally present.)

The following lists give the more interesting, representative and indicator species on the 'Cascades' and the passage beds. In addition, *Cryptogramme crispa* and *Phegopteris dryopteris* are representative (and the former abundant) scree plants in Cwm Cau, and *Erica cinerea* var. *alba* also occurs about the 'Cascades'. Many common lowland and upland species have been omitted from all the lists. Calcicole or mainly calcicole species in all lists are shown by the sign *cl*.

(1) *Cascades* (460–520 m., southerly aspect)

Alchemilla alpestris
cl Arabis hirsuta
Asplenium adiantum-nigrum
Campanula rotundifolia
Chrysanthemum leucanthemum
Filipendula ulmaria
Hypericum pulchrum
Lathyrus montanus
Oxalis acetosella

Populus tremula
Polystichum aculeatum f. lobatum
Primula vulgaris
Saxifraga hypnoides
Sedum roseum

cl Neckera crispa
cl Trichostomum tortuosum

(2) *Craig Cau* (500–600 m., easterly aspect)

Anemone nemorosa
Alchemilla alpestris
Adoxa moschatellina
cl Arabis hirsuta
Cystopteris fragilis f. dentata
Crepis paludosa
Centauria nigra
Chrysanthemum leucanthemum
Cochlearia alpina
Digitalis purpurea
Filipendula ulmaria
Geum rivale
Luzula maxima

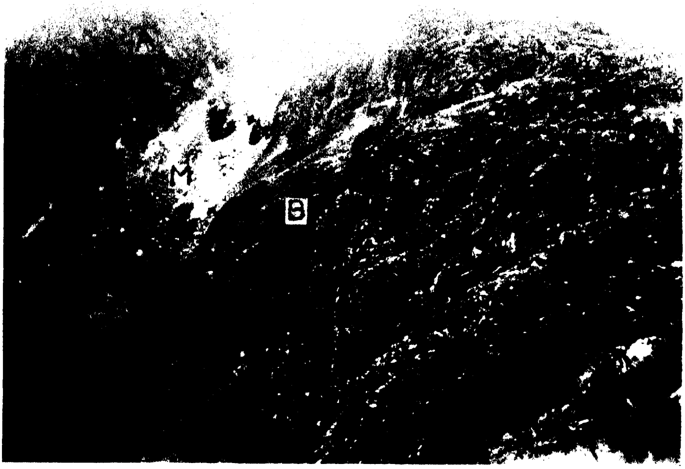
cl Meconopsis cambrica
cl Oxyria digyna
Oxalis acetosella
Saxifraga hypnoides
S. stellaris
Sedum roseum
Scilla non-scripta
Succisa pratensis
cl Thalictrum minus
Trollius europaeus

cl Neckera crispa
cl Trichostomum tortuosum

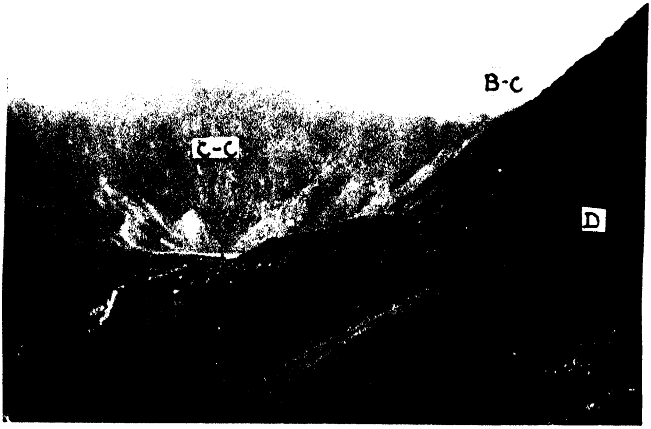
(*b*) *Cwm Geu Graig* (Pl. 2, phot. 1)

This is an incomplete corrie with steeply sloping floor, without the usually attendant corrie lake, situated at the extreme eastern end of the Cader Range. Like Cwm Cau it is carved out of the mudstones, but unlike that cwm it is only the width of the mudstones—about 150 m. The close proximity, however, of the south-facing dip slope of Upper Basic Volcanic rocks (with some dolerite intrusions) to the north-facing 'scarp' of the 'passage beds' and Upper Acid Volcanic rocks (often undercut) makes it an area of considerable ecological interest. The floor, at the top, is mostly open scree with an abundance of *Cryptogramme crispa*, but at the bottom passes into a close community of *Vaccinium myrtillus*. *Oxyria digyna*, in drier portions at the top of the scree, had tap roots 30 cm. in length.

The north-facing slope is less imposing than the south-facing one, but it is wetter and has overhanging rocks, which emphasize the shade. This may account for the presence



Phot. 1. Cwm Geu Graig, showing acid (A) and basic (B) volcanic rocks with intervening mud-stones (M).



Phot. 2. Cwm Cau (C–C), Bwlch Cau (B–C) and Llyn Cau in the valley bottom.

here of calcicolous species, but there is a strong suspicion that the rocks here—at least at the base of the slope—are also somewhat calciferous (cf. Cwm Cau).

List of plants (460–610 m.):

(1) *South-facing slope*

Anemone nemorosa
Antennaria dioica
cl Cystopteris fragilis f. dentata
Epilobium angustifolium
Galium verum
Genista pilosa
Lathyrus montanus
cl Melica nutans
cl Oxyria digyna
Primula vulgaris
Rosa mollis
Saxifraga stellaris
Sedum purpureum
S. roseum
Serratula tinctoria
cl Thalictrum minus
Teucrium scorodonia
Ulex gallii

(2) *North-facing slope*

cl Arabis hirsuta
cl Asplenium viride
cl Cystopteris fragilis f. dentata
Digitalis purpurea
Luzula maxima
cl Oxyria digyna
Saxifraga hypnoides
Sedum roseum
Succisa pratensis
cl Thalictrum minus

cl Neckera crispa
cl Trichostomum tortuosum

(*c*) *Tyrau Mawr*

Tyrau Mawr is a prominent peak near the western end of the great escarpment composed of ashes of the Upper Basic with dolerite intrusions. The ashes are less calciferous than the lavas (which are the most calciferous rocks in the Cader Idris sequence—Cox & Wells, 1927), and many distinctly calcicole species are hardly to be expected here. Nevertheless, the rocks have a moderately rich though varied flora, with a large number of lowland species. The determining factor appears to be the physical one, as on Craig Cau, though the flora here is not nearly as rich (excepting lowland species) as in that locality. Lower down the slope between Tyrau Mawr and the old trackway (Ffordd Ddu) the lower basic volcanic rocks made their appearance but, as the rock development is not good here, few species of calcicolous flowering plants occur, though calcicole lichens and mosses are frequent.

List of plants (530–610 m., northerly aspect):

Alchemilla alpestris
Anemone nemorosa
Angelica sylvestris
Campanula rotundifolia
Chrysanthemum leucanthemum
Chrysosplenium oppositifolium
Cryptogramme crispa
Cirsium lanceolatum
Digitalis purpureum
Filipendula ulmaria
Festuca ovina f. vivipara
Luzula maxima
Oxalis acetosella
Melampyrum pratense
Phegopteris polypodioides
cl Pimpinella saxifraga
Rhinanthus crista-galli
Sagina procumbens
Saxifraga hypnoides
S. stellaris
Sedum roseum
Succisa pratensis
cl Thalictrum minus
Thymus serpyllum
Urtica dioica
Valeriana dioica
cl Peltigera canina

Lowland plants also present include spp. of *Cerastium, Euphrasia, Hieracium, Solidago, Veronica, Viola, Dryopteris*, etc.

(d) Craig-y-Benglog

To the east and north-east of Cader Idris the Basic Volcanic rocks occupy lower ground. In the valley of the Wnion they are covered by glacial deposits or are cut off by branches of the Bala Fault, but they reappear on higher ground (but not so high as in the Cader area) on the north side of the valley, taking a trend to the north along the southern and eastern flanks of the old volcanic cone of Rhobell Fawr (860 m.). The Lower Basic are doubtfully present (or are very thin), but the Upper Basic are well developed, and at Craig-y-Benglog they form a precipitous rock face resembling in some respects (on a small scale) the dip slope of Cwm Cau. The rock is composed of ashes and pillow-lavas with dolerite intrusions. The area is of ecological interest not only because of the varied flora of the rock face (460–490 m.) and that of the gorge of the river Eiddon below (*c.* 300 m.), but because of the presence on its south-western flank of an upland ashwood (*Fraxinetum calcicolum*).

A general survey of plants of these two areas, rock face and ashwood, will now be given.

(1) *The rock face* (*c.* 1500–1600 ft., southerly aspect):

Alchemilla alpestris
Angelica sylvestris
cl Arabis hirsuta
Asplenium adiantum-nigrum
A. Ruta muraria
Cotyledon umbilicus-veneris
Digitalis purpurea
Epilobium montanum
Euphorbia amygdaloides
Filipendula ulmaria
cl Helianthemum nummularia f. tomentosum (in the gorge, 1000 ft.)
Hypericum pulchrum
Jasione montana
Lonicera periclymenum
Lathyrus montanus
Linum catharticum
Luzula maxima
Orchis mascula
Origanum vulgare
Lepidium smithii
cl Pimpinella saxifraga
Primula vulgaris
cl Selaginella selaginoides (in the gorge)
Sedum anglicum
S. purpureum
Succisa pratensis
Teucrium scorodonia
Thymus serpyllum
Ulex gallii
Urtica dioica
Valeriana dioica

cl Hypnum molluscum
cl Neckera crispa
cl Reboulia hemisphaerica (in the gorge)

The rock is rich in lowland species most of which have been omitted from this list. Dwarf trees (oak, ash, aspen, mountain ash) are present in small numbers as well as such shrubs as hazel, rose, holly, bramble and hawthorn.

It is interesting to note that about 60 years ago the farmer introduced a few goats to eat the herbage on the rock which is dangerous to sheep. Since then the goats have increased in number to such an extent (25–30) and have 'run wild' so that their destructiveness (breaking fences, etc.) tends to outweigh their usefulness (see under 'upland ashwood').

The rock face is separated from the gorge by unstable scree which is mostly devoid of vegetation. A transition from bare scree, through *Rhacomitrium*-covered scree to 'grass with pteris' may be seen in some parts. Though *Calluna vulgaris*, *Erica cinerea* and *Vaccinium myrtillus* may be seen sparingly on the rock they are generally absent from the scree. *Phegopteris dryopteris* may be found here as a scree plant. Lower down the stream *Scolopendrium vulgare* grows rather luxuriantly and, in the village of Rhydymain, *Ceterach officinale* (which is very local in the Dolgelly district) grows on mortared stone walls.

(2) *The upland ashwood.* This wood is a little more than 13 acres (5·35 hectares) in extent at an altitude of 270–380 m. (900–1250 ft.), with a southerly aspect. Though often

present as a constituent member of the dominant oakwoods (characterized chiefly by *Quercus sessiliflora*) or as individual trees or very small communities near the streams, the ash rarely forms communities of any size in this district. In this case, ashwood is developed partly on scree and partly on the rocky slope and appears to be of recent origin, probably having seeded from ashes in the oakwoods (now largely cleared) on the lower ground. It is said that within living memory (? 60–70 years) there was here only a hazel scrub with a few small ashes.

The woodland falls into two more or less distinct parts according to the nature of the ground, viz. a western part of moderately steep slope consisting of large block scree with occasional bedrock exposed, and an eastern part of steep slope whose upper portion consists largely of precipitous bedrock and the lower of scree in all stages of formation. In between is a much smaller area of rather open land which passes into hill pasture toward the top. The soil is everywhere rather scanty, occurring in 'pockets' between the blocks of the scree, on ledges, or in depressions in the bedrock, or as a thin layer of mature scree. Towards the bottom of the slope there is in most parts an increase in depth of soil.

Structure and composition. The average height of the dominant trees is about 15 m. and the girth about 0·9 m. The distance between the trees averages some 4·5 m. so that the wood is rather open, including some quite open spaces, and contains numerous shrubs. *Quercus sessiliflora* occurs chiefly in the lower part of the wood, on the deeper soil. The only individual *Euonymus* present has been 'barked' (probably by goats) and is in bad condition. The woody species are:

Fraxinus excelsior	d.	Quercus sessiliflora × robur	o.
Betula pubescens var. glabrata	r.-o.	Tilia cordata	v.r.
Quercus sessiliflora	o.	Ulmus glabra	r.-o.
Corylus avellana	l.d.	Prunus spinosa	o.-f.
Crataegus monogyna	o.-f.	Rosa canina	r.-o.
Euonymus europaeus	v.r.	Sorbus aucuparia	o.
Hedera helix	l.	Lonicera periclymenum	r.-o.

The ground vegetation falls into three more or less distinct communities: (1) on very thin soil over rock or incompletely overgrown scree giving a dry habitat, (2) on comparatively thin soil of medium dampness; and (3) in wet or marshy places. *Helianthemum* is confined to the top of wood (*c.* 380 m.).

(1) *On rocks and screes incompletely overgrown:*

cl R Arabis hirsuta	l.	Linum catharticum	o.
Asplenium trichomanes	o.	Lotus corniculatus	o.-f.
Cardamine hirsuta	o.	*cl* R Melica nutans	r.
cl C. impatiens	o.-f.	*cl* Origanum vulgare	l.a.
R Cotyledon umbilicus-veneris	o.	RT Polypodium vulgare	o.
Deschampsia flexuosa	o.	Potentilla erecta	o.-f.
Epilobium montanum	o.	Rumex acetosella	o.
Euphrasia sp.	l.	Saxifraga hypnoides	l.
Festuca ovina	o.	Sedum anglicum	o.-f.
Galium aparine	o.	Sedum forsterianum	l.
R Galium saxatile	f.	S. purpureum	l.
Geranium lucidum	l.	Teucrium scorodonia	l.a.
G. robertianum	o.-f.	Thymus serpyllum	l.a.
Hieracium pilosella	o.	Veronica officinalis	l.
H. sylvaticum	o.		
cl Helianthemum chamaecistus f. tomentosum	r.-o.	*cl* R Necktera crispa	o.
		Rhacomitrium lanuginosum	l.d.
Jasione montanum	l.	*cl* Trichostomum tortuosum	o.
R Lathyrus montanus	o.	Peltigera sp.	o.

R = on rocks; T = on trees.

(2) *Soil of medium dampness:*

Agrostis tenuis	l.a.
Ajuga reptans	o.
Alchemilla vulgaris	l.
Anthoxanthum odoratum	l.a.
Arrhenatherium elatius	f.
Asperula odorata	l.a.
Athyrium filix-femina	o.
Bellis perennis	o.
Blechnum spicant	o.
Brachypodium sylvaticum	o.-f.
Campanula rotundifolia	l.
cl Cardamine impatiens	o.-f.
Carex binervis	o.
Caucalis anthriscus	o.
Centaurea nigra	o.
Cerastium vulgatum	o.
Circaea lutetiana	l.a.
Conopodium majus	o.-f.
Cynosurus cristatus	o.-f.
Dactylis glomerata	f.
Digitalis purpurea	r.-o.
Dryopteris felix-mas	o.-f.
D. montana	f.
Epilobium montanum	o.-f.
Fragaria vesca	o.-f.
Geum urbanum	o.-f.
Holcus lanatus	o.
Hypericum montanum	o.
Hypochaeris radicata	l.
Lapsana communis	o.-f.
Melampyrum pratense	l.
Melandrium dioicum	o.
Mercurialis perennis	l.a.-l.d.
Nepeta hederacea	l.a.
Oxalis acetosella	f.
cl Pimpinella saxifraga	o.
Poa trivialis	f.
Primula vulgaris	o.-f.
Prunella vulgaris	f.
Pteridium aquilinum	l.a.
Rumex acetosa	o.
Rubus fruticosus	o.
R. idaeus	o.
Sanicula europaea	l.a.
Scilla non-scripta	l.
Solidago virgaurea	o.
Stachys arvensis	o.
Stellaria holostea	o.-f.
S. media	o.
Succisa pratensis	o.
Urtica dioica	l.a.
Veronica chamaedrys	o.
Vicia sepium	o.
Viola riviniana	f.

In these long lists it will be observed that besides several 'exacting' and many indifferent species there are a few attached to acid soils, doubtless to be explained by the local accumulation of humus in this wet climate, which may have a rainfall of 70–80 in. (180–200 cm.). The *p*H values obtained show marked though not extreme acidity, from 4·7 to 5·6.

(3) *Wet or marshy places:*

Cardamine pratensis	l.
Cirsium palustre	o.
Chrysosplenium oppositifolium	l.
Crepis paludosa	l.
Deschampsia caespitosa	o.
Ficaria verna	l.
Fraxinus excelsior (seedlings)	o.
Galium palustre	l.
Juncus articulatus	l.
Juncus conglomeratus	l.
Lotus uliginosus	o.
Lysimachia nemorum	o.-f.
Mentha aquatica	o.
Myosotis scorpioides	l.
Ranunculus flammula	l.
R. repens	o.-f.
Trollius europaeus	l.
Valeriana dioica	f.

Calluna and *Vaccinium myrtillus* are absent from the general ground flora though they are present with *Erica cinerea* in small quantities on the rocks in the upper part of the wood. The varied nature of the ground flora is attributable to the operation of several important factors, viz. the presence of calciferous rocks, together with pockets of acid soil developed in the humid climate, the open nature of the woodland and the great diversity of the screes. In the upper part of the wood the soil has not collected in sufficient quantity to support healthy full-grown trees. Stagheaded, dead, and uprooted trees are rather frequent. This, together with the absence of seedling ashes of any size, seems to point to degeneration and possible reversion to hazel scrub. The situation of the woodland at the extreme upper limit of trees, where the winter conditions are often very severe (as in 1936–7 when the weight of snow caused many of the branches to be torn off the trunks) and the presence of goats (about twenty to thirty in number) which frequent the wood, devour the seedlings and strip the bark off the branches, are additional destructive factors. The hazel, which is the pioneer shrub, is abundant in most parts, but from the lower portion much has been cut to provide wood for fencing. At the bottom of the wood where the slope is gentle and the soil deeper than on the upper parts, oaks are rather frequent.

In correspondence with the high rainfall, mosses are abundant in the ground layer of the wood, forming a carpet on the boulders of the block scree and on the bedrock. The presence of such plants as *Frullania tamarisci*, *Hypnum molluscum*, *Madotheca platyphylla*, *Neckera crispa*, *Trichostomum tortuosum* which are calcicolous (or mainly so) point to the calciferous nature of the bedrock.

(*e*) *The Llyn Gafr and Llyn Aran rocks*

These two localities have been described in the previous paper. The Gafr rocks form part of the pillow lava band of the Lower Basic to the south of Llyn Gafr, and the Aran rocks are on the lavas of the Upper Basic on the southern or south-eastern side of Cwm Aran.

The Lower Basic volcanic group is not particularly calciferous in its (geologically) lower parts but becomes increasingly so towards the upper parts where, in the pillow-lava band, are the most calciferous rocks in the Cader area. On the other hand, the Upper Basic volcanic group has different facies (chiefly ashes or lavas) in different localities and as has already been stated the lavas are more calciferous than the ashes. There are remains of old lime kilns near these calciferous rocks. There is one in fair preservation near Bwlch Coch in the Cader area and there are remains of kilns of very simple construction in the Craig-y-Benglog district. It is said that *calch llwyd* (= grey lime) was obtained by burning these rocks and that this was spread on the fields.

The *distinctiveness* of the flora of the pillow-lava band (which stretches for some miles at the foot of the great escarpment except where broken by incipient corrie action or covered by morainic material and which in parts may only be a few yards in width) as compared with that of contiguous rocks, and the *richness of the vegetation* of the basic rocks of Cwm Aran as against the stark nakedness of the granophyre on its western wall, are two of the most striking ecological features in the whole of the Cader country. Where the lava is poorly developed only cryptogamic species may occur; but these are generally calcicolous species such as *Asplenium viride* (where the band is not below about 450 m.), *Hypnum molluscum*, *Neckera crispa*, *Peltigera canina*, *Peltidia aphthosa*, *Solorina saccata*, *Reboulia hemisphaerica*.

(*f*) *The acidic rocks*

In contrast to the richness of the flora of the localities mentioned above, stands the poverty of that on the acidic rocks in general, of which the granophyre of the great escarpment may be taken as an example. This great rampart is the most conspicuous, and excepting Craig Cau, the most imposing rock structure in the Cader country. This great sill stretches from the Cyfrwy (saddle) for a distance of about 3 miles to, and including, the laccolite of Mynydd Moel. The percentage of CaO in granophyre 'Eurite', Llyn-y-Gader, Cader Idris, is given as 1·94 (Cole & Jennings, 1889). Contrast with this the percentage of CaO (11·10) in variolite from the outer part of a 'pillow' from the lavas of the Upper Basic at Craig-y-Benglog (Dr H. F. Harwood, analyst). Owing to its columnar structure and to its chemical composition the granophyre is largely devoid of vegetation; but in parts where there are moist flat ledges (or near the runlets) where soil has collected there is a fair amount of vegetation consisting chiefly of distinct calcifuge species. The following list is fairly representative of such places (see also Price Evans, 1932, p. 38):

Alchemilla alpestris
Calluna vulgaris
Cryptogramme crispa
Erica cinerea
Euphrasia spp.
Hieracium spp.
Galium saxatile
Luzula maxima
Narthecium ossifragum
Potentilla erecta
Pinguicula vulgaris
Rumex acetosella
Solidago spp.
Saxifraga stellaris
Sedum roseum (very occ.)
Sedum anglicum
Succisa pratensis
Vaccinium myrtillus.
Agrostis sp.
Deschampsia flexuosa
Festuca ovina f. vivipara
Carex flava
Phegopteris polypodioides
Lomaria spicant
Lycopodium alpinum
L. clavatum
Rhacomitrium lanuginosum
Sphagnum sp.

Most of these species may be found in pockets of acid soil or on the dolerites among the basic volcanic rocks; but the characteristic species of the last mentioned rocks are absent from the acidic rocks.

PLANT RECORDS

The following rare plants have been recorded for Cader Idris. Those marked with an asterisk are included in Druce's *Comital Flora* as occurring in Merionethshire; the others are new or presumably lack recent confirmation. Most of these records date from the latter half of last century, i.e. before Cader Idris had been surveyed in accordance with modern geological practice. Thus, details concerning the nature of the bed-rock could hardly be expected. The later records are more complete in this respect, but the main interest of the list lies in the number and variety of rare (some very rare) species recorded for such a relatively small area. Interesting records include:

Adiantum capillus-veneris, Llyn Gafr and Cwm Aran, on basic volcanic rocks; *Arenaria verna*; **Asplenium germanicum*, above Llyn Cau; **A. septentrionale*, under the saddle or cyfrwy; **Genista pilosa*, Mynydd y Gader, on dolerite and acid volcanic rocks; *Juniperus communis*, Cwm Aran rocks; **Malaxis paludosa*, in sphagnum bogs under Tyrau Mawr; **Rubus saxatilis*, rocks above Llyn Cau; **Salix herbacea*, near the summit; *S. reticulata*, near the summit; **Saussurea alpina*, Cwm Aran rocks; *Silene acaulis*, Cwm Cau; **Woodsia ilvensis*, above Llyn Aran; *Hypnum turgescens*, in *Hypnum commutatum* community near Llyn Gafr; *Pertusaria monogona*, on dolerite, Mynydd y Gader.

Most of the plants in the above list are difficult to find on Cader Idris to-day; but that is not to say that they are not there or that any record was made in error. The story of the records concerning *Genista pilosa* is sufficient warning in this direction. Bingley, in his *Tour round North Wales* (1800), recorded it from 'the foot of Cader Idris, between Dolgelley and Llyn Aran, about half a mile from the pool'. J. E. Bowman, is quoted in *The New Botanist's Guide to the localities of the rare plants of Britain*, by H. C. Watson, London (1835–7) as saying: 'I could not find it in the recorded situation near Cader Idris.' Watson, in his *Topographical Botany* (1883), writes, 'an error'. The plant was rediscovered in 1901 in quantity on the rocks near Mynydd Moel (Cader Idris). In 1930 it was found by the writer, and his wife, in several places on the dolerite and acid volcanic rocks of Mynydd y Gader.

Very young plants of *Adiantum capillus-veneris* were found by the writer on calciferous lava near Llyn Gafr and in Cwm Aran, and the identification was confirmed at Kew.

Several attempts have since been made to find this fern but without success. The record must then rank as unconfirmed.

Asplenium septentrionale occurs in fair quantity on the rocks in the gold-mining area north of Dolgelley and *Arenaria verna* has been recorded from the same locality.

In a letter to the writer (the late) Mr John Griffith, Headmaster of the Dolgelley Grammar School, stated that he had found one bush of *Juniperus communis* on the rocks above Llyn Aran and that the nearest spot where he had seen it, north of 'Cader', was on Moel Meirch, above Llyn Edno (Caernarvonshire).

Druce includes a record of *Salix reticulata* in his *Comital Flora* with the remark: 'The Cader Idris record is most doubtful' (see also Price Evans, 1932, p. 39, footnote).

In regard to *Hypnum turgescens*, I extract the following from Dixon's *Handbook of British Mosses*, 3rd ed. 1924: '...Its recent discovery in Britain is especially interesting because it was a native of our islands in Pleistocene times, and supposed to have become extinct. Dr Nathorst discovered it in 1872 in the Arctic Freshwater Beds from a well at Munderley, Norfolk, in company with *Salix polaris*....It has been happily discovered in a second locality, when the Brit. Bryol. Soc. met at Dolgelley in 1922; it was not recognized at the time but some stems of it were later detected by Rev. R. Jackett among bog mosses gathered on the side of Cader Idris.'

Up to the present Cader Idris is the only British record for the rare lichen *Pertusaria monogona*. 'It is very interesting to note that in addition to the "warted" form already recorded), the rarer, somewhat plane areolate form of this lichen, is also present. Both forms occur in good quantity, sometimes on the same boulder, but the plane areolate form seems to be the more abundant in this locality (the reverse seems to be true of the relative frequency of the two forms on the Continent)' (Price Evans, 1932).

SUGGESTIONS CONCERNING FIELDWORK, ETC.

The following suggestions for work in the field on the vegetation of Cader Idris and its vicinity may now be made (in merest outline) with statements of some of the problems. Investigation is required of the following:

(1) The cryptogamic flora of the lavas, the pillow-lavas and the ashes of the Upper and Lower Basic Volcanic rocks. The geological maps (Cox, 1925; Cox & Wells, 1927) form excellent bases for work of this nature—not only on the extrusive rocks but on the intrusives as well.

(2) The invasion of the Alpine zone (550–900 m.) by lowland plants—the study of the factors involved in their distribution and of the modifications they undergo, i.e. the study of how a plant becomes 'an Alpine'. For example, how does the *Trollius* of Craig Cau at 550 m. differ from that growing in the zone of cultivation, where it is locally abundant. Similarly, how does the *Chrysanthemum leucanthemum* growing on the rock face north of and just under the summit (*c.* 890 m.) differ from that in lower regions or the *Rhinanthus crista galli* of Tyrau Mawr (*c.* 535 m.) from that of the meadows and pastures of the zone of cultivation?

(3) The study of the 'relict flora'. [Are these plants spreading or dying out?] In 1800 Bingley recorded *Saxifraga oppositifolia* from Craig Cau, and in 1877 Pearce recorded it from the Aran rocks—Cwm Aran. Is this plant present in these localities to-day? It is relatively abundant on the Llyn Gafr rocks.

(4) The influence of *aspect* on plant distribution and growth. [As the Cader Range runs

east to west, with a steep north-facing scarp slope and a dip slope much dissected into minor 'scarps', there is ample opportunity for such work.]

(5) The study of *shade* plants and 'lair' flora [small caves—'solution caves'—are present in parts of the pillow-lava band, on the pillow-lavas of Cwm Aran, and in the passage beds in Cwm Geu Graig and Cwm Cau].

(6) The influence of *water* on the distribution of floristically rich localities. Though Cader Idris is a region of high rainfall (*c.* 150 in., 380 cm.) it is also subject to strong winds as well as to low temperature in winter and at night. Rich localities seem to be determined—apart from the presence of available lime in the rocks—by an ample supply of 'head' water from the rocks above.

(7) The study of the effect of *grazing* on the upland communities [by isolating suitable sections].

(8) The part played by birds in *regional* distribution. Cader Idris is near the important west coast spring migration route and much of its surface is 'open'. Did *Genista pilosa* reach Cader in this way? The only other recorded locality for it in Wales is Pembrokeshire—also on the same route.

(9) The study of the '*passage beds*' between the Llyn Cau mudstones and the Upper Acid Volcanic rocks.

(10) Outside the Cader area, the study of the flora of the Upper Basic Volcanic Rocks of the Rhobell Fawr district. Though the (Ordovician) volcanic sequence is less complete in the Rhobell district than on Cader Idris, and the rocks are at a lower elevation, this area, together with the centre of the Dome itself, is virgin ground to the ecologist.

(11) The effect of *goats* on vegetation. As already indicated, Craig-y-Benglog and more especially the Benglog ashwood give ample scope for this kind of study to-day. There are no goats on Cader Idris, though at one time, not so long ago, they must have been present; in the *Cambrian Tourist's Guide and Companion* (Atkins, 1847, Dolgelley) there occurs this reference to Craig Cau: 'Craig Cai: Its sullen and majestic front was only enlivened with patches of the moss saxifrage, and a few goats of pure white who were skipping carelessly along its dangerous steeps.'

SUMMARY

The floristically rich localities in the *Cader Idris* and *Rhobell Fawr* districts of south-west Merionethshire are situated on or about the Basic Volcanic series of rocks which form part of the 'ring-fence of volcanoes' on the southern and eastern flanks of the Harlech Dome. These rocks are chiefly composed of lavas (including pillow-lavas) and ashes with dolerite intrusions and intercalations of slaty material. The determining factor is the presence of lime in a form readily available for plants, but certain physical factors such as the presence of a 'head' of water (preferably dripping water), and of ledges and 'pockets' of good soil on the precipitous rock-faces are also of considerable importance. The most calciferous rocks of these series are the pillow-lavas which have vesicles filled with calcite: the lavas in general are more calciferous than the ashes. In contrast to the fertility of these rocks stands the sterility of the acidic rocks of which the granophyres (intrusives) and the rhyolites (of the acid volcanic series) may be taken as examples. In between these two extremes are the ashy slates, the mudstones and the dolerites. A number of rare (chiefly phanerogamic) species have been recorded by botanists from the Cader Idris area, but the presence of some of them, to-day, needs confirmation. In recent years these

two districts (Cader Idris and Rhobell Fawr) have been the subjects of thorough geological investigation and the papers on them (Cox & Wells, 1921; Cox, 1925; Wells, 1925) provide excellent bases for ecological work of one kind or another.

These notes, on Cader Idris and Craig-y-Benglog, were compiled, in part, during the period 1926–32: being on localities outside the selected transect they were not included in my 1932 paper but reserved for a future occasion. Circumstances, however, have not favoured further work and the results of the investigation (for which the writer takes full responsibility) must, thus, be regarded as tentative. They are given (with suggestions, etc.) in the hope that they may be of some use to future workers in this field.

The writer wishes to express his sincere thanks to Prof. A. G. Tansley and Prof. A. Hubert Cox for their invaluable help in connection with this and the previous paper on Cader Idris and district; to (the late) Dr J. H. Salter for the names of most of the rare (or locally rare) plants in the list under 'plant records' (p. 176) and to Mr Albert Wilson for the identification of some of the mosses. Finally he would like to thank Mr Robert Richards and Miss Richards of Benglog Farm for their kindness during many visits to Craig-y-Benglog.

I wish to record also a correction in my earlier paper (Price Evans, 1932):
For *Conium maculatum*—pp. 36 and 37—read *Angelica sylvestris*.

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THE VEGETATION OF THE SAND DUNES OF THE CAMEL ESTUARY, NORTH CORNWALL

By IAN HEPBURN

(*With Plate* 3 *and one Figure in the Text*)

A considerable number of papers have already appeared, describing the vegetation occurring on sand dunes in the British Isles, and the pioneer stages in the colonization of mobile dunes seem to conform generally to a well-marked type. When, however, the sand has become partially fixed, a large number of non-maritime species are able to gain a foothold, and in this stage the composition of the vegetation as it passes into 'fixed dune' shows a great variety in the areas which have been studied. The species occurring must clearly depend to a large extent on the proximity of seed parents and also on the power of a particular species to survive in sand which is still partially mobile. The ultimate vegetation must also be influenced by the nature of the sand. The front dunes in all areas which have been studied seem to be generally alkaline, largely as a result of their salt content. Where the sand contains little $CaCO_3$, however, the older dunes tend to become acid and the subsequent vegetation is accordingly influenced. The chief interest in the present study lies in the fact that the sand, even in the oldest and most fixed portions of the area, is always highly calcareous and contains at least 50% $CaCO_3$, with a *p*H exceeding 8·0. The other feature of interest about these Cornish dunes is that they include a well-defined area of dunes which have recently been formed and whose age is known with some accuracy. These dunes show the early stages of colonization very clearly.

It will be seen from the lists of species included in this paper that this area is no exception in supporting a very varied flora, including some species which do not seem to have been recorded from similar habitats elsewhere. An analysis of the vegetation occurring on more or less fixed dunes in a number of localities in the British Isles and Ireland has been included at the end of this paper. This list, besides showing something of the great variety of the flora, shows that a number of non-maritime species occur in this type of habitat with considerable regularity.

It had been hoped to include in this paper studies of the more extensive sand-dune areas along the north Cornish coast, at Perranporth and elsewhere, but transport difficulties have unfortunately made this impossible.

The area studied is situated on the east side of the Camel estuary on the coast of north Cornwall, opposite the little port of Padstow (see Fig. 1). The front of the dunes extends from a point just south of Brea Hill to the village of Rock, a distance of about 1½ km. Behind this is a large area of fixed dune and blown sand, which extends in some places for a distance of over 1 km. from the water's edge and reaches as far north as Daymer Bay. The blown sand covers, usually thickly, an area of slate or diabase, and much of it lies over 30 m. above the sea. The vegetation of the whole blown-sand area is very similar to that on the lower lying fixed dunes nearer the sea, which were more intensively studied for the detailed lists in this paper. Much of the blown-sand area is occupied by the St Enodoc Golf Course, with the result that the vegetation on the fairways and greens has been considerably modified.

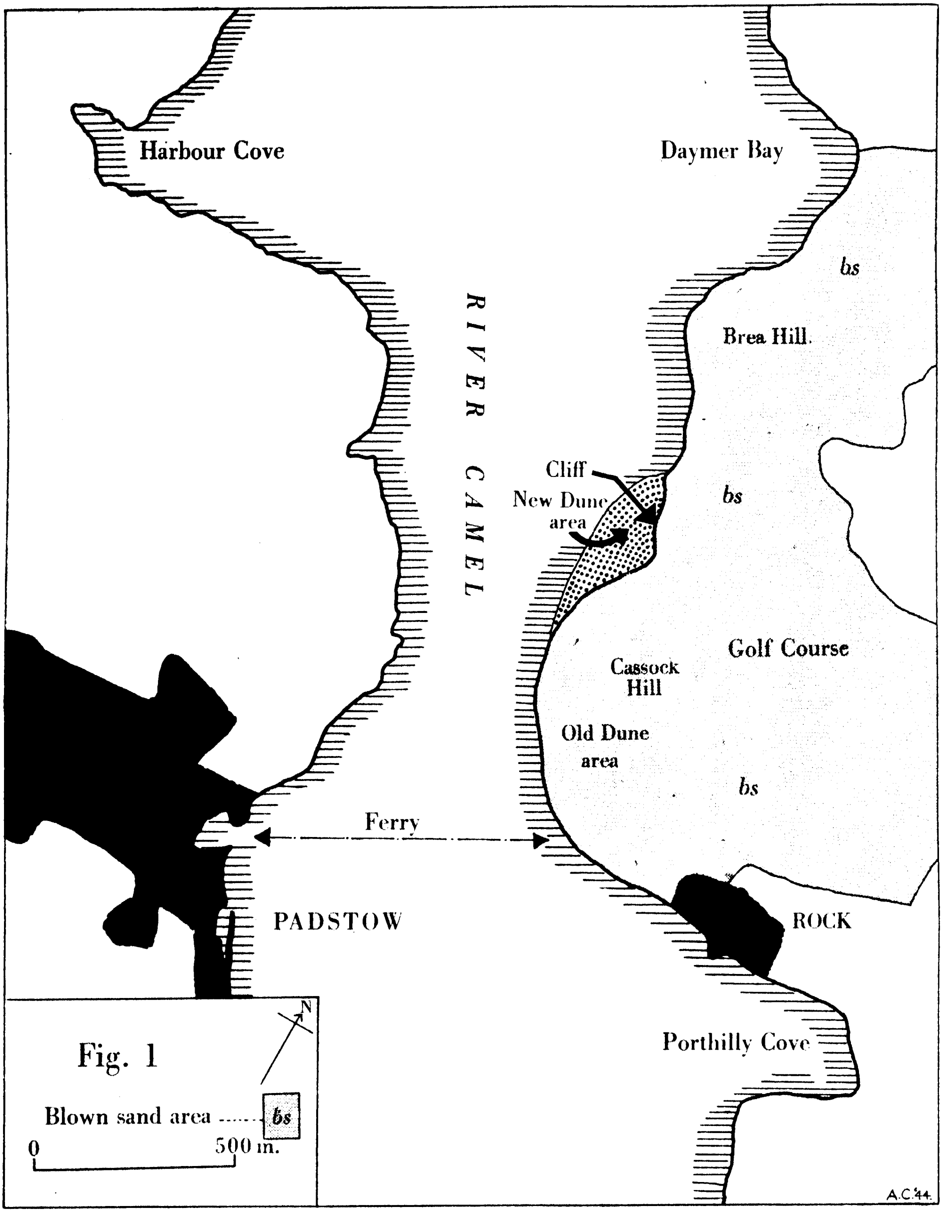


Fig. 1

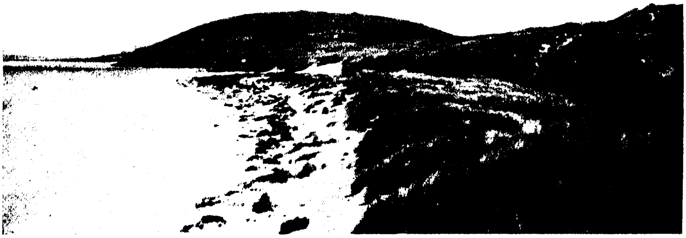
Harbour Cove
Daymer Bay
RIVER CAMEL
bs
Brea Hill.
Cliff
New Dune area
bs
Golf Course
Cassock Hill
Old Dune area
bs
Ferry
PADSTOW
ROCK
Porthilly Cove
N
Blown sand area .... bs
0
500 m.
A.C.'44.

The area marked in Fig. 1 as 'new dunes' consists of a stretch of open *Ammophiletum* which has been forming in the little bay just south of Brea Hill, joining up with the older dunes at a point 200–300 m. north of the usual terminus of the Padstow ferry. The age of these dunes is known fairly accurately. In 1923 there were no dunes here and a sandy beach sloped gently up to the foot of a low slate cliff, which is still visible at the western edge of the blown-sand area. Shortly after this date, banks of sand began to accumulate in this bay and became colonized by *Ammophila*. A photograph taken in 1930 shows a considerable area of low dunes formed, and another taken in 1933 (Pl. 3, phot. 1) shows a further extension seawards. The 1943 photograph (Pl. 3, phot. 2) shows their present extent and there is some reason to suppose that, for the present, no further growth is taking place, since the high spring tides seem to be washing the sand away slightly from the roots of the front *Ammophila* plants at the southern end. In addition, the society of strand plants in front of the dunes was not so prominent in 1943 as in many previous years.

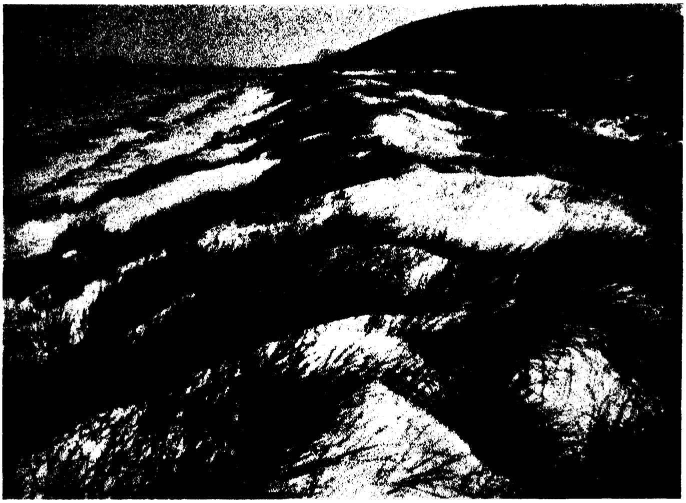
The older dunes, which join this area to the south, do not at present show much of the usual open *Ammophiletum* in front, since the seaward side of the dunes is being washed away rapidly. The 'fixed-dune' area thus extends right up to high-water mark, and its edge now forms a considerable sand cliff. This cliff extends for a considerable distance along the seaward face and is as much as 7 m. high in places. It is strewn with the debris of fixed-dune vegetation, including scrub plants such as *Crataegus monogyna* and *Prunus spinosa*, which have fallen from the top of the cliff, and also with the relics of elaborate barbed wire entanglements which were erected in 1940. The recent rapid erosion which has been taking place here is largely due to a shift in the course of the main channel of the Camel river, which took place some time in 1940 and caused the river to keep to the east side of the estuary until it reaches a point below the ferry bottleneck. Some measurements made with posts erected near the edge of the dunes in 1942–3 suggest that the annual rate of erosion along some portions of the front of the dunes during this period has been as much as 25 m. As a result of this, there is at present no sign of the usual 'strand' community along most of the length of these dunes, and the patches of 'open' dunes are largely limited to occasional 'blow-outs'. It is likely that the present phase of erosion is quite temporary, for as recently as 1920 new dunes were being formed and colonized close to the ferry, and much more recently there was a well-marked 'strand' community all along the front of these dunes. The tides through the narrow ferry gap are very strong, and the sand-banks in the estuary are continually changing. If the main river channel should once more shift across the estuary, young dunes will undoubtedly grow up in front of the present eroded western face of the older dunes.

NATURE OF THE SAND

The sand of the north Cornwall coast is very rich in calcium carbonate. During recent years very large amounts of sand have been removed from the Camel estuary as a source of lime for agricultural purposes. The amount of $CaCO_3$ in the estuary sand varies considerably and is reputed to be over 80% at Harlyn Bay. The samples taken over the dune area considered in this paper all showed over 50% of $CaCO_3$, and specimens from an older range of dunes in the golf-links area, nearly 1 km. from the shore, were found to contain nearly 70%. The *p*H in all cases showed markedly alkaline conditions even in the surface layers. With such universally high amounts of $CaCO_3$ in the sand there was, of course, no sign of a modification in the vegetation as a result of the leaching of



Phot. 1. 'New dunes' area in 1933.



Phot. 2. 'New dunes' area in 1943.

carbonates from the surface layers, as has frequently been noticed in dunes elsewhere. The following average results were obtained from specimens taken from different positions in the area:

Locality	% $CaCO_3$	*p*H
From shore in front of first line of 'new dunes'	53·9	8·3
Top 5 cm. from 'fixed-dune' area	55·6	8·4
Surface sand from 'blow-outs' on old range of dunes, 35 m. above the sea and ¾ km. from the shore	68·8	8·5
Top 5 cm. from blown-sand area farthest from the sea (nearly 1 km.)	51·7	8·0

Mr. C. Diver has pointed out that another reason for the maintenance of the high $CaCO_3$ content is the exceedingly dense snail population of the whole area, particularly of *Helicella acuta*, but also of *Cepaea nemoralis*, *Helix aspersa*, etc. As these occur very much more thickly on the old dunes than on the new ones, this may account in some measure for the higher carbonate content in the older dunes.

It was noticed that the sand taken from the surface of the fixed-dune area immediately below the mosses and other vegetation was appreciably darker in colour, but only in the top layer. It was clear that this effect was largely due to the remains of quite recent vegetation which had not yet passed into humus. The amount of humus that accumulates in the sand is actually very small. This is to be expected, since it is well known that an open sandy soil and a high $CaCO_3$ content furnish the best conditions for the oxidation of organic matter.

Some determinations of the humus content of various samples of sand taken from near the surface in the 'fixed-dune' area were carried out. In each case the dry sample was freed as far as possible from recent organic remains by sieving, and the amount of humus was then determined by the loss in weight obtained on treatment with strong hydrogen peroxide solution. The amounts of organic matter found varied betwen 0·25 and 0·85%.

VEGETATION OF THE NEW DUNES

The area of new dunes which, as has already been mentioned, are not more than 20 years old, affords an interesting study of the progressive colonization of mobile sand. The front line of low dunes (Pl. 3, phot. 2) is about 500 m. long and the breadth of the strip from the original cliff to the front dunes is just over 100 m. at its widest point. The initial colonization has been entirely carried out by *Ammophila*. There is a small patch of *Agropyrum junceum* above the cliff face and this has produced a few seedlings at the northern end of the area, but it has clearly played no part in the building up of the dunes generally. The top of the present front line of dunes is on the average only about 4 m. above the level of high water. There are remains of several older ridges behind these, but they are very irregular and quite low.

In front of the dunes there is the usual unstable community of foreshore plants. As has already been mentioned, this was more sparse in 1943 than in previous years, owing to the slight erosion of the front of the dunes. *Salsola kali* was the only species present in quantity, but the following plants were also noticed in this and previous years. The order given below is approximately that of their frequency (reading across):

Salsola kali	Atriplex patula
Cakile maritima	A. glabriuscula
Euphorbia paralias	Beta maritima

In addition, on the shore of Daymer Bay, just north of Brea Hill, and in front of the very small strip of *Agropyretum* which occurs at the western end of the little Porthilly inlet to the south, *Honckenya peploides*, *Polygonum raii* and *Calystegia soldanella* also occur.

The front of the dunes for an average distance of 8 m. from the seaward edge bears no vegetation except *Ammophila* in the constantly shifting sand. At about this distance back, where the low fore-dunes can give a little protection from the prevailing westerly winds, the first colonists begin to appear. The following list gives an idea of the composition of this variable community in the strip about 8–14 m. from the front of the dunes, where the surface sand is still too mobile to be colonized by mosses. In places the plants occur, temporarily at any rate, quite thickly, but there is much bare sand. The list is arranged in the approximate order of frequencies (reading across):

First colonists

Senecio vulgaris	Senecio jacobaea
Taraxacum erythrospermum	Leontodon nudicaulis
Crepis capillaris	Cerastium semidecandrum
Cirsium arvense	Sonchus asper
Arenaria serpyllifolia	Erodium cicutarium
Cerastium tetrandrum	Rumex crispus
Euphorbia paralias	Oenothera biennis
Tussilago farfara	Cynoglossum officinale
Cakile maritima	Matricaria maritima
Carlina vulgaris	Anagallis arvensis

At a distance of about 14 m. on the average from the edge, the first colonizing moss makes its appearance, in this case *Bryum pendulum*, and occasionally *B. capillare*. The effect of this is to stabilize much more fully the surface sand, and it is clearly an important factor in the development of the vegetation. In the older fixed dunes these species are rarely seen, since they have been choked out by the close-growing vegetation and other more strongly growing mosses, but here they cover large areas. From this point to the eastern edge of the new dunes the vegetation becomes progressively closer, though it still remains open and there is a good deal of bare sand. With a few exceptions, the majority of the species characteristic of the adjacent fixed dunes now make their appearance, and the vegetation of some patches has the same general appearance as that on the fixed dunes. There is, however, no *Festuca arenaria* except on the southern edge near the old dunes, and the two mosses, *Brachythecium albicans* and *Tortula ruraliformis*, which are so characteristic of the fixed dunes, though they are well established near the cliff, do not form the dense carpets that are seen all over the fixed dune area. One or two small patches of the lichen, *Peltigera canescens*, which is sometimes such a prominent feature of sand dunes, were noticed both here and in the fixed-dune area. The amounts seen were, however, so small that it clearly plays no important part in the stabilization of the sand.

In order to gain an idea of the relative frequencies of the commoner species in this area where the mosses are becoming established and the surface of the sand is largely stabilized, fifty 1 ft. squares (⅓ m.) were taken at random over the area, and the different species occurring within them were noted. If the number of squares in which a particular species occurs is doubled, a specific frequency percentage can be obtained. Owing to the incomplete colonization of this area, this method is not so useful here as it is on the more stable fixed dunes, where the vegetation is more regular, but it gives a more accurate order of frequency than could be obtained by inspection. Since the growing periods of the various species cover a wide range of time, two separate counts were carried out, one in the spring and one in July. The results for those species which appeared in both counts, actually the majority, were averaged. The average number of species occurring in each square was 10.

The following are the results of the counts arranged in descending order of frequency:

	%
Ammophila arenaria	96
Senecio vulgaris	72
S. jacobaea	68
Leontodon nudicaulis	66
Arenaria serpyllifolia	58
Crepis capillaris	54
Hieracium pilosella	52
Taraxacum erythrospermum	
Myosotis collina	42
Valerianella olitoria	36
Daucus gummifer	24
Cerastium semidecandrum	22
Tussilago farfara	
Hypochoeris radicata	18
Cirsium arvense	16
Veronica arvensis	
Arenaria leptoclados	14
Cerastium tetrandrum	
Sonchus asper	
Carex arenaria	12
Carlina vulgaris	
Erodium cicutarium	
Inula squarrosa	10
Rumex crispus	

	%
Blackstonia perfoliata	8
Centaurium umbellatum	
Euphorbia paralias	
Lotus corniculatus	
Rubus spp.	
Sedum anglicum	
Cirsium lanceolatum	6
Cynoglossum officinale	
Erophila verna	
Matricaria maritima	
Oenothera biennis	
Phleum arenarium	
Agropyrum junceum	4
Anthyllis vulneraria	
Bellis perennis	
Erigeron acre	
Geranium molle	
Teucrium scorodonia	
Trifolium dubium	
Clematis vitalba	2
Eupatorium cannabinum	
Galium mollugo	
Holcus lanatus	
Dactylis glomerata	
Verbascum thapsus	

The bryophytes were also included in the counts and gave the following frequencies:

	%		%
Bryum pendulum	48	Bryum capillare	14
Tortula ruraliformis	42	Trichostomum flavovirens	6
Brachythecium albicans	36	Barbula convoluta	4

The following species, which did not appear in the squares, were also noted in the area:

Agrimonia eupatoria
Cakile maritima
Euphorbia portlandica
Ligustrum vulgare
Plantago coronopus
Rumex acetosa
Sonchus oleraceus
Anagallis arvensis
Centaurea nigra
Hedera helix
Linum catharticum
Poa loliacea
Sonchus arvensis

It is remarkable that a number of species which showed high frequencies in the fixed dune vegetation were not noted at all on the young dunes, and it must be concluded that these species are amongst the later colonizers of this habitat. The chief of these are:

Euphrasia occidentalis
Galium verum
Ononis repens
Sherardia arvensis
Veronica chamaedrys
Festuca arenaria (one place near edge)
Luzula campestris
Plantago lanceolata
Thymus serpyllum
Viola riviniana

VEGETATION OF THE FIXED DUNES

The area of the older fixed dunes, which lie to the south and east of the new dunes, is decidedly more extensive. The front dunes have a coast-line of nearly 1 km. from the beginning of the new dunes to the village of Rock, and behind them is a rather narrow strip of genuine fixed dune, which in recent years has been considerably broader. Behind this to the east and also to the north lies a much larger area of blown sand which forms a deposit, generally thick, over the rising ground and reaches a height of over 35 m. above the sea. The whole of this irregular area must cover some 200 hectares (500 acres), and much of it is occupied by the St Enodoc Golf Course. There is a general upward slope from the shore facing to the west or south-west, and behind this much of the area consists of an irregular plateau of an average height of 35 m. above the sea. There are various unconnected ranges of old dunes in the blown-sand area, some of these reaching a height of nearly 15 m. above the general level. The dunes rising from sea-level on the shore side are not so high and are also irregular. The vegetation of the blown-sand area does not differ extensively from that of the front dunes except in a few places where the sand deposit is thin and the rock lies close to the surface, or where a fairway or green on the golf course has modified it by mowing.

Ammophila occurs all over the area, but where the vegetation has become close, it has been largely choked out. In most of this area it is clearly not happy and rarely flowers. There are, however, a number of places where the vegetation is not very close, and here *Ammophila* continues to thrive and to flower freely. It is particularly luxuriant round the various 'blow-outs' in the higher dunes, some of which form natural bunkers on the links.

The whole district is infested with rabbits, and even the new dune area is rapidly becoming populated. Many of the plants have obviously been nibbled, and the general shortness of the vegetation is more due to this cause than to exposure to the strong winds. This has made the identification of the grasses difficult, but there can be no doubt that, unless the sward has been modified by mowing, *Festuca arenaria* is the only grass present in any quantity and is dominant. *Holcus lanatus* has become established in some places, generally in the hollows, and is the next most common grass. *Carex arenaria* is also much in evidence in many places.

The two mosses, *Brachythecium albicans* and *Tortula ruraliformis*, are extremely prominent in the vegetation and are also very persistent, remaining an important ingredient of the mown fairways of the golf links. The pioneer species of *Bryum*, noticed on the new dunes, have become almost completely choked out in the fixed-dune area.

Amongst the front dunes, the incipient formation of scrub can be seen. This would doubtless have progressed farther if the area had not been exposed to such powerful westerly winds. Since there are no high dunes to act as a wind-break to a hollow behind them, and the blown-sand area rises behind in a gradual slope to over 35 m., very little protection is afforded for the development of scrub plants. Small patches of *Prunus spinosa* and *Crataegus monogyna* are found in the lower hollows. Frequent patches of *Clematis vitalba* trailing over the ground are also a prominent feature of these front dunes. Much of the scrub on the front dunes has recently been eroded away.

The general flora of the fixed dunes is rich and, as would be expected, shows a number of calcicolous species. It is curious that the very characteristic calcicole, *Linum catharticum*, was infrequent in this area, though it is known to be common on the Perranporth dunes. On the other hand, *Teucrium scorodonia* is an unexpected inhabitant. Most of the species are low growing, but in August the whole area is very bright with *Senecio jacobaea*, and other tall-growing plants such as *Inula squarrosa*, *Cynoglossum officinale*, the thistles *Cirsium arvense* and *lanceolatum*, and the rare *Scrophularia scorodonia* are prominent.

A close inspection of the vegetation reveals a very large number of seedlings of many species competing with each other for space to grow, with *Festuca arenaria*, though always present, not unduly prominent. A percentage frequency count was carried out for the fixed dunes in exactly the same way as has been already described for the new dunes. The samples were chosen almost entirely from the lower dunes near the shore, and the modified vegetation of the golf links was avoided. The high percentage frequencies shown in the list illustrate the very large number of plants which occur, the average number of different species per square being over 15.

List of fixed dune species

	%
Festuca arenaria	92
Senecio jacobaea	84
Galium verum	82
Ammophila arenaria	78
Crepis capillaris	76
Leontodon nudicaulis	64
Luzula campestris	62
Viola riviniana	
Veronica chamaedrys	54
Taraxacum erythrospermum	44
Plantago lanceolata	42
Geranium molle	34
Lotus corniculatus	
Thymus serpyllum	
Carex arenaria	32
Cirsium arvense	
Hieracium pilosella	
Sherardia arvensis	
Hypochoeris radicata	30
Cerastium semidecandrum	28
Trifolium dubium	24
Erodium cicutarium	22
Euphrasia occidentalis	
Cirsium lanceolatum	20
Ononis repens	18
Teucrium scorodonia	
Trifolium repens	
Bellis perennis	16
Holcus lanatus	
Inula squarrosa	
Arenaria serpyllifolia	14
Cerastium tetrandrum	

	%
Myosotis collina	14
Valerianella olitoria	
Carduus tenuiflorus	12
Carlina vulgaris	
Prunella vulgaris	
Veronica arvensis	
Cynoglossum officinale	10
Ranunculus bulbosus	
Arenaria leptoclados	8
Erophila verna	
Ranunculus parviflorus	
Senecio vulgaris	
Daucus gummifer	6
Erigeron acre	
Nepeta hederacea	
Sedum anglicum	
Sonchus asper	
S. oleraceus	
Agrimonia eupatoria	4
Blackstonia perfoliata	
Centaurium umbellatum	
Clematis vitalba	
Dactylis glomerata	
Lithospermum officinale	
Phleum arenarium	
Scrophularia scorodonia	
Euphorbia paralias	2
E. portlandica	
Linaria repens	
Prunus spinosa	
Rubus spp.	
Trifolium procumbens	

Only three bryophytes appeared in the counts, but four others were noticed in the area:

	%		%
Brachythecium albicans	78	Tortula ruraliformis	56
Bryum pendulum (in barer places)	4		

and

Barbula convoluta
B. vinealis
Bryum capillare
Trichostomum flavovirens

The following other species, which did not appear in the squares, were also found in the area:

Achillea millefolium
Agropyrum pungens
Anthriscus vulgaris
Centaurium pulchellum
Erodium moschatum
Festuca rigida
Gentiana amarella
Kentranthus ruber
Linum catharticum
Oenothera biennis
Poa pratensis
Reseda luteola
Rumex acetosa
R. crispus
Salvia verbenaca
Valeriana sambucifolia
Agropyrum junceum (one small patch)
Agrostis alba
Centaurea nigra
Erodium maritimum
Eryngium maritimum
Foeniculum vulgare
Heracleum sphondylium
Ligustrum vulgare
Lycopsis arvensis
Plantago coronopus
Polygala vulgaris
Rosa micrantha
Rumex acetosella
Sagina procumbens
Spiranthes spiralis
Verbena officinalis

The many other common grasses which have appeared in the modified vegetation of the golf links have not been included in the above lists.

COMPARISON WITH OTHER DUNES

Salisbury has shown (**14**, **15**) that a number of the early colonists of blown sand and the younger dunes are calcicolous plants, no matter what amount of carbonate is originally present in the sand, and that these species generally persist for a considerable time in the more consolidated dunes. If the original amount of $CaCO_3$ contained in the sand is small, the surface sand will tend gradually to become acid owing to the leaching of the carbonates in the surface layers. A vegetation consisting of calcifuge plants will therefore begin to appear and this may eventually develop into sandy heathland as at Blakeney, Studland, Southport, and elsewhere. The chief difference to be noticed in very calcareous dunes, such as these at Rock, is that the leaching is not sufficient to have any appreciable effect on the very large amounts of $CaCO_3$ present in the sand, with the result that the vegetation over the whole area remains similar and retains a markedly calcicolous bias.

Since there are no areas of wet 'slacks' at Rock, there is no formation of dune marsh, which is such a frequent feature of many dunes in other parts of the country.

A study of the literature concerning sand-dune vegetation reveals the fact that a very large number of species occur in this habitat in different localities. In fifteen localities which were considered it was found that over 250 different species, exclusive of bryophytes, were listed as occurring on more or less fixed dunes. It is clear that a large number of these are plants which grow in other habitats in the neighbourhood of the dunes and find conditions in the dunes equally suitable for their requirements, while they are persistent enough to compete with earlier colonists. The presence of many of these plants will therefore be largely fortuitous and will depend chiefly on the types of vegetation occurring in the immediate neighbourhood of the dunes. There are, however, a number of plants which occur with some regularity on most sand dunes, and these may be grouped into two classes: (i) true dune plants, which are practically never found except on dunes or sandy shores; (ii) plants which are found just as frequently in other habitats but appear as regular ingredients of the sand-dune vegetation.

The species belonging to the first class form a comparatively short list and most of these are pioneer colonists on shifting sand, which often do not persist in the close vegetation of the fixed dunes. Certain plants which are more characteristic of the 'strand' of fore-dune community, but which also occur frequently on the open dunes, have been included in the list below. Those which appear to be confined to the fore-dunes, such as *Salsola kali*, have not been included. The following seem to be the chief species:

Agropyrum junceum
Cakile maritima
Carex arenaria
Eryngium maritimum
Euphorbia portlandica
Honckenya peploides (also frequently on shingle)
Ammophila arenaria
Calystegia soldanella
Elymus arenarius
Euphorbia paralias
Festuca arenaria

with some rarer species such as:

Brassica monensis
Thalictrum dunense
Corynephorus canescens
Viola curtisii

The plants belonging to the second class are much more numerous and are more difficult to assess. An attempt has been made below to draw up lists of the most characteristic species which occur on more or less fixed dunes in the British Isles and Ireland.

These have been drawn as far as possible from areas where subsequent modification of the vegetation to dune heath, dune marsh, dune pasture, etc., has not yet occurred, though owing to the great variety of intermediate types, this restriction cannot have been enforced very strictly. It has also been rather difficult to find a sufficiently large number of localities for which reasonably complete lists are available. Eight localities have been chosen finally out of a considerable number of sand-dune studies which were available, and the comparative list below contains all the species which are listed as occurring in 50 % and over of these localities.

The following are the details of the localities which have been used, together with such information concerning the $CaCO_3$ content and acidity as were available and the appropriate references:

No.	Locality	Average *p*H	Average $CaCO_3$ %	Reference
1	Rock, north Cornwall	8·3	55·5	—
2	Braunton Burrows, north Devon	7·5	13·5	W. Watson (**22**, **23**), F. R. Elliston Wright (**2**)
3	Burnham and Berrow, Somerset	—	*c.* 3	C. E. Moss (**8**), H. Stuart Thompson (**19**), W. Watson (**23**)
4	Formby and Southport, south Lancs	7–7·4	2–3	F. E. Weiss (**24**), E. J. Salisbury (**14**), W. G. Travis (**20**), C. T. Green (**4**)
5	Portrush and Portstewart, north Antrim and Derry	7–7·5	4–5	C. D. Chase (**1**)
6	Ayreland of Bride, Isle of Man	6·9	0·75	E. J. Moore (**7**), J. W. Hartley & J. A. Weldon (**5**)
7	Blakeney Point, Norfolk	6·8	Under 0·5	F. W. Oliver & E. J. Salisbury (**9**), E. J. Salisbury (**15**)
8	Culbin Sands, Elgin	Acidic	—	D. Patton & E. J. A. Stewart (**11**, **12**)

It has been decided not to make any attempt to indicate frequencies, since these were not available for all the above localities, and in any case were not likely to conform to the same standard. The areas considered cover a wide range of $CaCO_3$ content, but it will be seen that in this relatively early stage in colonization the differences in the most frequent species occurring in the various localities are not very marked. It is noticeable, however, that in two of the acidic areas, Blakeney and Ayreland of Bride, both of which appear to have been fully listed, the actual number of species occurring is considerably less. The dune plants of the first class, which persist in the fixed-dune areas, have also been included in the lists.

List of species occurring in 50 % *and over of the localities*

	1	2	3	4	5	6	7	8	
	Rock	Braunton Burrows	Burnham and Berrow	South-port	North Antrim	Isle of Man	Blakeney	Culbin	Total occur-rences
Achillea millefolium	×	×	×	×	×	.	.	×	6
Agrostis alba	×	×	×	.	×	.	.	×	5
Aira caryophyllea	.	×	×	×	×	×	.	×	6
A. praecox	.	×	×	×	×	.	×	×	6
Ammophila arenaria	×	×	×	×	×	×	×	×	8
Anacamptis pyramidalis	.	×	×	×	×	.	×	.	5
Anagallis arvensis	.	×	×	.	×	.	×	.	4
Arenaria serpyllifolia	×	×	×	×	×	×	.	.	6
Bellis perennis	×	×	×	.	×	×	.	×	6
Blackstonia perfoliata	×	×	×	×	.	.	.	.	4
Carduus tenuiflorus	×	×	×	.	×	×	.	.	5
Carex arenaria	×	×	×	×	×	×	×	×	8
Carlina vulgaris	×	×	×	×	.	.	.	.	4

List of species occurring in 50 % *and over of the localities* (continued)

	1 Rock	2 Braunton Burrows	3 Burnham and Berrow	4 South-port	5 North Antrim	6 Isle of Man	7 Blakeney	8 Culbin	Total occur-rences
Centaurium pulchellum	×	×	×	×	.	.	.	.	4
C. umbellatum	×	×	×	×	×	.	.	×	6
Cerastium semidecandrum	×	×	×	×	×	×	×	×	8
C. tetrandrum	×	×	×	×	×	×	×	×	8
C. vulgatum	×	×	×	×	×	×	×	×	8
Cirsium arvense	×	×	×	×	×	.	×	×	7
C. lanceolatum	×	×	×	×	×	.	×	×	7
Crepis capillaris	×	×	×	.	×	.	.	×	5
Cynoglossum officinale	×	×	×	×	.	.	.	.	4
Echium vulgare	.	×	×	×	.	.	.	×	4
Equisetum arvense	.	.	×	×	×	.	.	×	4
Erigeron acre	×	×	×	×	.	.	.	.	4
Erodium cicutarium	×	×	×	×	×	×	×	×	8
E. maritimum	×	×	×	.	.	×	.	×	5
Euphorbia paralias	×	×	×	×	.	.	×	.	5
E. portlandica	×	×	.	×	×	.	.	.	4
Euphrasia spp.	×	×	×	×	×	×	.	×	7
Festuca arenaria	×	×	×	×	×	×	×	×	8
Filago germanica	.	×	×	.	×	.	.	×	4
Galium verum	×	×	×	×	×	×	×	×	8
Geranium molle	×	×	×	.	×	.	×	.	5
Hieracium pilosella	×	×	×	.	×	×	×	×	7
Holcus lanatus	×	×	×	×	×	.	.	×	6
Hypochoeris radicata	×	×	×	.	×	×	×	×	7
Leontodon autumnale	.	×	×	×	×	.	.	×	5
L. nudicaulis	×	×	×	×	×	×	.	.	6
Linum catharticum	×	×	×	×	×	.	.	×	6
Lotus corniculatus	×	×	×	×	×	×	.	×	7
Luzula campestris	×	×	.	×	×	.	×	×	6
Lycopsis arvensis	×	×	×	.	.	.	.	×	4
Matricaria inodora	×	×	×	.	×	×	.	×	6
Myosotis collina	×	×	×	×	×	×	×	.	7
M. versicolor	.	×	×	×	.	.	×	×	5
Oenothera biennis	×	×	×	×	.	.	.	.	4
Ononis repens	×	×	×	×	.	×	.	.	5
Phleum arenarium	×	×	×	×	×	×	×	.	7
Plantago coronopus	×	×	.	×	×	×	×	×	7
P. lanceolata	×	×	×	.	×	.	.	×	5
Polygala spp.	×	×	.	×	×	×	.	×	6
Potentilla anserina	.	×	×	×	×	.	.	×	5
P. erecta	.	×	×	×	×	.	.	×	5
Prunella vulgaris	×	×	×	×	×	.	.	×	6
Reseda luteola	×	×	.	×	×	.	.	.	4
Rosa spp.	×	×	×	×	×	×	.	×	7
Rubus spp.	×	×	×	×	×	.	×	.	6
Rumex acetosella	×	×	.	.	×	.	×	×	5
R. crispus	×	×	×	×	×	.	×	×	7
Sagina procumbens	×	×	×	×	×	.	.	×	6
Sedum acre	.	×	×	×	×	×	×	.	6
Senecio jacobaea	×	×	×	×	×	×	×	×	8
S. vulgaris	×	×	.	×	.	×	×	×	6
Sherardia arvensis	×	×	×	.	×	.	×	.	5
Sonchus arvensis	×	×	×	.	.	.	.	×	4
S. asper	×	×	×	.	×	.	.	×	5
S. oleraceus	×	×	×	.	×	.	.	.	4
Taraxacum erythrospermum	×	×	×	×	×	×	×	.	7
Teucrium scorodonia	×	×	×	.	.	.	.	×	4
Thymus serpyllum	×	×	×	×	×	×	.	×	7
Trifolium dubium	×	×	×	.	×	×	.	×	6
T. repens	×	×	×	×	×	.	.	×	6
Valerianella olitoria	×	×	×	.	×	×	×	.	6
Veronica arvensis	×	×	×	.	×	.	×	×	6
V. chamaedrys	×	×	×	.	×	.	.	×	5
V. officinalis	.	×	.	.	×	.	×	×	4
Viola canina	.	×	×	×	.	×	.	×	5

During the compilation of the above list, the dune flora of a number of other localities was examined, and though the available lists were clearly not so complete, it was apparent that a very large proportion of the species in the above list were characteristic of these areas also. Since this list has been produced on information from a relatively small number of areas, some reasonably frequent species must have just escaped inclusion. As these species may be as typical as many of those which occur in only 50 % of the chosen localities, it has seemed advisable to add a supplement to include these. A further short list has therefore been evolved which contains those additional species which are listed in at least four of any of the areas for which any information was available. Information from seven further localities has been used for this purpose, in addition to that from the eight original ones, though some of these have produced few species other than those which appeared in the first list. The relevant details for the additional areas are as follows:

No.	Locality	Average *p*H	Average $CaCO_3$ %	Reference
9	Dog's Bay, near Roundstone, Co. Galway	8·1	75	A. G. Tansley (**17**)
10	Rosapenna, Co. Donegal	8·3	48·6	A. G. Tansley (**18**)
11	Kenfig Burrows, Glamorgan	'Calcareous'	—	M. Y. Orr (**10**)
12	Holme, Norfolk	—	2–3	A. S. Marsh (**6**), S. M. Wadham (**21**)
13	Mouth of Tay, Fife and Forfar	Acidic	—	W. G. Smith (**16**)
14	South Haven, Studland, Dorset	Acidic	—	R. Good (**3**)
15	Walney Island, Barrow	6–6·5	—	W. H. Pearsall (**13**)

Additional list

Anthyllis vulneraria
Filago minima
Gentiana amarella
Hypochoeris glabra
Potentilla reptans
Ranunculus bulbosus
Rumex acetosa
Sambucus nigra
Sedum anglicum
Spiranthes spiralis
Verbascum thapsus
Viola curtisii

Campanula rotundifolia
Galium saxatile
Gentiana campestris
Koeleria cristata
Radiola linoides
Ranunculus repens
Sagina nodosa
Saxifraga tridactylites
Senecio sylvaticus
Trifolium arvense
Vicia lathyroides

The two lists together show the richness and the variety of the flora of this habitat and, despite the fortuitous nature of many dune species, it is clear that there is a considerable constancy in the composition of the vegetation in various localities. Nearly all dune areas appear to have their local specialities, and certain special characteristics of wider areas can sometimes be observed. Thus the prevalence of *Rosa spinosissima* in the north-west areas and the occurrence of *Iris foetidissima* on both sides of the Bristol Channel are characteristic of dunes in widely separated localities in the same general area.

The Cornish dunes considered in the present study show no less than sixty-two out of the seventy-eight typical species in the first list, and at the same time support a few local specialities such as *Scrophularia scorodonia*, *Linaria repens*, *Clematis vitalba*, etc., which do not appear in any of the other lists.

In conclusion, the author would like to express his thanks to (the late) Mr H. N. Dixon for determining the mosses, to Dr Mackenzie Lamb for determining the lichen, to the Moulton Agricultural Institute for verifying the *p*H readings, to Mr A. Constant for drawing the map, and to Prof. A. G. Tansley for his help and advice.

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THE INFLUENCE OF SOIL REACTION ON ROTATION GRASS IN SOUTH-WEST SCOTLAND

By R. LAIRD, *The West of Scotland Agricultural College*

In previous issues of the *Journal of Ecology*, E. Wyllie Fenton has discussed the influence of intensive manuring and rotational grazing on the composition of the swards of old grasslands (**1**), the influence of seed mixture on grasslands in south-east Scotland (**2**), and grassland retrogression in Devonshire permanent pastures (**3**). His studies of older grasslands in Devon showed that intensive manuring and rotational grazing improved the flora, resulting in the production of swards containing 70–80% *Lolium perenne* and *Trifolium repens*, with 5% *Agrostis*, 5% *Poa trivialis* and with small quantities (less than 3% of each) of *Dactylis glomerata*, *Ranunculus* sp., *Bellis perennis* and *Hieracium* sp. The percentage of *Agrostis* in the original sward is not stated, although at the commencement of treatment it apparently averaged less than 13% of the sward.

In his investigations affecting grassland retrogression in Devonshire permanent pastures he reviews how transition from Group 1 pastures (*Lolium perenne* and *Trifolium repens* dominant) to Group 2 pastures (*Trifolium repens* dominant and *Agrostis* subdominant) and to Group 3 pastures (*Agrostis* dominant and *Holcus lanatus*, *Cynosurus cristatus* or *Anthoxanthum odoratum* subdominant) and to lower groups, or vice versa, may take place. He finds the chief deficiency of most permanent pastures to be phosphate and lime. Such pastures also often suffer from inefficient management and inadequate grazing.

In his botanical survey of grasslands in the east of Scotland he found that the botanical composition of grasslands which have been recently sown are, other things being equal, determined by the seed mixture. With similar seed mixtures, strongly similar grasslands will, he states, be obtained, and the use of an inferior strain of any species may cause marked changes in the flora. In most of the analyses quoted for rotation grass, *Lolium perenne* and *Trifolium* sp. comprise approximately 80% of the species present, *Lolium perenne* predominating in the first year and *Trifolium repens* in the later years. In only one case was there an appreciable proportion of *Agrostis* sp. In only a few special cases also did *Agrostis* occur in appreciable quantities in the permanent pasture swards, and in most of these *Trifolium repens* was dominant. He also comments that in natural or semi-natural grasslands skilful management will produce improvement, that acidity is one of the commonest causes of inferior vegetation, and that although the geological formation and the nature of the surface soil may be a decisive factor in determining the flora under natural conditions, this is not necessarily true of all agricultural land. He concludes that, 'In grasslands of long duration, soil conditions and general treatment play a very important part: grazing is a most important biotic factor. Deficiency in nitrogen, calcium, phosphorus or potassium or of more than one of these, is reflected in the flora of the grassland.'

In the view of Wyllie Fenton, therefore, the nature of the grass-seed mixture is the most important factor affecting the composition of the sward in rotation grass. He found, however, that in grassland of long duration soil conditions—manuring, liming, drainage, etc.—and general management play a very important part. He states that fertility and other conditions in soils under rotation cropping are generally favourable to the establishment of the superior sown species of herbage plants.

During the past twenty years I have had many experiences in the seeding of grasslands which contrast strongly with those of Wyllie Fenton. In these the composition of the seed mixture proved of far less importance than the soil status in regard to lime and phosphate in influencing the botanical composition of the sward. Particulars of a number of these cases are given with the results obtained. The ten-point quadrat method was employed in making the botanical analyses hereinafter quoted.

HUNTERSTON DEMONSTRATION AREA, WEST KILBRIDE

A very acute case of lime deficiency was encountered on cropping land at Hunterston, West Kilbride, where a demonstration area of 7½ acres was maintained from 1923 till 1926. The *p*H value of the soil was in the region of 4·0, and no definite results were being obtained from manures, unmanured plots in 1923 equalling in yield those to which liberal dressings of manure had been applied. The cropping results have been given by the writer in a College bulletin (**4**), published in 1930. Lime was applied to five-eighths of the area in 1924 and to a further quarter in 1925. Liming (1 ton CaO per acre) in 1924 increased the yield of main-crop potatoes from 5·55 to 12·95 tons per acre; swedes were increased from 6·25 to 23 tons; and in 1925 the oat yield was raised from 9·5 to 14·25 cwt. grain per acre. In 1926 the hay yield on the unlimed areas averaged 16 cwt. per acre, and on the limed land 40·25 cwt. per acre. After the hay crop had been cut in 1926, the *p*H values were determined and found to average as follows (by quinhydrone electrode):

Unlimed	1 ton CaO	1¾ tons CaO
3·86	4·59	5·43

A portion of the area hitherto unlimed was then limed, and a gradual improvement took place on this newly limed section. The land lay under pasture till the end of 1932, at which time a number of botanical analyses were made with the following results on the various sections:

	1¾ tons CaO on roots	1 ton CaO on roots	1 ton CaO after hay	Unlimed	Mixture A 1 ton CaO	Mixture B 1 ton CaO	Mixture C 1 ton CaO
Lolium perenne	21	15	8	3	20	22	18
Dactylis glomerata	4	8	15	2	6	—	1
Phleum pratense	1	1	—	—	1	—	—
Festuca duriuscula	10	9	9	2	10	12	13
Cynosurus cristatus	21	19	16	7	22	23	25
Poa pratensis	12	11	11	4	12	12	9
Holcus lanatus	5	6	15	21	5	5	7
Agrostis spp.	5	6	10	1	20	19	20
Musci	1	3	4	—	2	3	2
Juncus effusus	—	—	2	2	—	—	—
Ranunculus repens	1	—	—	—	—	—	—
Trifolium repens	19	22	10	1	20	19	20

It is clear that the seed-mixture effect was negligible in comparison with the previous soil treatment. Particulars of the standard seed mixture used and of the other three mixtures referred to are as follows (in lb. per acre):

	Standard	A	B	C
Lolium perenne	14	8	26	6
L. italicum	6	4	10	18
Dactylis glomerata	8	8	3	6
Phleum pratense	2	3	1	2
Festuca elatior	3	4	1½	3
Avena elatior	—	5	2	—
Cynosurus cristatus	½	½	½	½
Poa pratensis	½	½	½	½
Festuca duriuscula	½	½	½	½
Trifolium pratense	3	3	3	2
T. hybridum	1	1	1	1
T. repens	1	1	1	½

On this land a potato crop was grown in 1933, followed by an oat crop in 1934 and potato crops in 1935, 1936 and 1937. On the unlimed strip each year, the crop was much poorer than on the remainder of the land. Similar effects on crops of lime applied as much as 20 years earlier has been reported by J. A. Hanley (**5**). Oats were again grown at Hunterston in 1938 and grass seeds sown. The influence of lime applied 14 years earlier was evident on the young seeds; the sward was much greener and had a higher clover content. In 1939 the influence of the lime treatment in the previous rotation was marked, and certain observations were made on the hay aftermath on the various plots in October 1939. Results were as follows (lime treatment and previous rotation indicated):

	1¾ tons CaO roots	1 ton CaO roots	1 ton CaO seeds	1 ton CaO after hay	Unlimed
	Botanical analyses				
Lolium perenne	38	25	36	38	10
Dactylis glomerata	30	32	35	32	17
Trifolium pratense	21	6	8	15	1
T. hybridum	6	3	3	3	—
T. repens	4	1	2	3	—
Holcus lanatus	1	8	4	—	8
Agrostis spp.	—	17	7	6	41
Rumex acetosa	—	8	5	3	23
	Herbage analyses (% dry matter)				
Nitrogen	2·24	1·52	1·82	2·03	1·51
P_2O_5	0·91	1·07	1·07	1·07	1·11
CaO	1·04	0·756	1·05	1·10	0·445
	Soil figures				
*p*H value	4·50	4·37	4·44	4·31	3·91
mg. 'available' P_2O_5 per 100 g. soil	41·4	34·5	31·3	42·3	33·3

All plots show a satisfactory phosphate figure. The greatest residual effect of the lime appears to be on the 1¾ tons CaO roots plot; 1 ton CaO after hay has produced a similar effect on the botanical and herbage analyses; the 1 ton CaO seeds is exerting more effect than the 1 ton CaO roots, which would sink farther in the soil in the earlier rotation. The nitrogen and P_2O_5 content of the herbage on the unlimed plot is similar to that of the 1 ton CaO roots plot, but the CaO content is much lower, even although the CaO content of the 1 ton CaO roots plot is much lower than of the other limed plots. The herbage on the unlimed plot consists of a much higher percentage, viz. 72, of inferior plants than on any of the limed plots, where the poorest plot is again the 1 ton CaO roots plot with 33% inferior plants. The *p*H value (3·91) of the unlimed plot is definitely lower than that of any of the limed plots.

MORRISTON DEMONSTRATION AREA, MAYBOLE

The experience on Morriston, Maybole, where a College demonstration area was maintained by the writer during 1932–6, is typical of those of many farmers, occupying similar cropping land. This soil was not so extremely acid as that on the Hunterston demonstration area, its *p*H value at the commencement of the trials in 1932 being 4·98. Lime applied at the rate of 1 ton per acre increased the total potato yield in 1932 from 12·02 to 12·64 tons per acre, while the swede yield was raised from 17·35 to 29·15 tons, and the mangold yield was increased fourfold from 5·8 to 23·2 tons: in the following year this liming only increased the grain yield of the oat crop from 35·0 to 36·6 cwt. per acre. The average hay yield in 1934 was 55 cwt. per acre on the limed sections (the range for various seed mixtures was between 53·9 and 58·8) as compared with 37·2 on the unlimed sections. A botanical analysis made of the hays on the limed sections of the areas sown with certain seed mixtures and on the unlimed portion gave the following results in July 1934 (S.M. = seed mixture, B.A. = botanical analysis):

									Unlimed	
	S.M. lb.	B.A. %	S.M. lb.	B.A. %	S.M. lb.	B.A. %	S.M. lb.	B.A. %	S.M. lb.	B.A. %
Lolium perenne	14	31	8	19	20	40	26	57	14	35
L. italicum	6	12	4	12	8	24	10	19	6	2
Dactylis glomerata	6	—	8	2	4	—	3	—	6	2
Phleum pratense	4	—	6	1	3	—	2	—	4	1
Cynosurus cristatus	1	7	1	2	1	1	1	5	1	1
Poa pratensis	1	2	1	6	1	1	1	3	1	1
Trifolium spp.*	4½	26	4½	13	4½	20	4½	14	4	1
Holcus lanatus	—	21	—	41	—	14	—	2	—	35
Agrostis spp.	—	1	—	2	—	—	—	—	—	11
Rumex acetosa	—	—	—	—	—	—	—	—	—	11

* *T. pratense* 3 lb., *T. hybridum* 1 lb., *T. repens* ½ lb.

It is apparent from the above figures that the proportion of rye grass in the sward was higher and that of the *Holcus* was lower where the larger seedings of rye grass were employed. It is evident also that the proportion of weeds was much higher, and of the clovers lower, where the land had not been limed.

A year later botanical analyses were again made with the following results for the various seed mixtures:

									Unlimed	
	S.M. lb.	B.A. %	S.M. lb.	B.A. %	S.M. lb.	B.A. %	S.M. lb.	B.A. %	S.M. lb.	B.A. %
Lolium perenne	14	29	8	20	20	27	26	27	14	—
L. italicum	6	—	4	—	8	—	10	—	6	—
Dactylis glomerata	6	25	8	31	4	21	3	14	6	5
Phleum pratense	4	4	6	7	3	5	2	2	4	1
Cynosurus cristatus	1	3	1	4	1	2	1	2	1	—
Poa pratensis	1	7	1	9	1	8	1	4	1	—
Trifolium pratense	3	5	3	1	3	4	3	5	3	2
T. hybridum	1	—	1	—	1	—	1	—	1	—
T. repens	½	22	½	23	½	25	½	27	½	4
Holcus lanatus	—	5	—	4	—	6	—	15	—	9
Agrostis spp.	—	—	—	1	—	2	—	4	—	70
Rumex acetosa	—	—	—	—	—	—	—	—	—	9

The botanical analyses differences have become much less during the year, the only significant difference being the amount of cocksfoot present, which is approximately proportional to the amount of seed in the mixtures employed. Serious deterioration of the sward has taken place on the unlimed land, where weeds total 88% of the sward against 5% weeds on the limed portions sown with the same seed mixture.

Further observations and botanical analyses made a year later, in September 1936, showed no visible boundaries between plots sown with the various seed mixtures, and that all seed mixtures were giving almost identical swards where the treatments were similar: the percentage of rye grass was around 28%, with the cocksfoot between 15 and 20% on the limed land. On the unlimed land the inferior plants had almost completely crowded out the useful types.

A section had been sown out with a seed mixture composed chiefly of grazing strains of the various plants, but otherwise similar to the standard mixture already referred to. The perennial rye grass was Kent indigenous, the cocksfoot was New Zealand Akaroa, and the timothy Aberystwyth S. 50. The hay yield in 1934 had been identical with that of the standard seed mixture, in which Ayrshire perennial rye grass, Danish cocksfoot, and Scotch timothy had been included, and during 1935 and 1936 there appeared to be very little difference in pasture yield between the two mixtures, although differences in appearance were visible at certain periods. It was accordingly decided that relative yields should be ascertained by taking cuttings at intervals of 4 weeks during the summer of 1937. Three cuttings were made between 14 May and 6 August from sections of the grazing strains plot and two adjoining commercial strains plots, and the yields and chemical analyses of the herbage determined. The yields were ascertained in respect of plots of an area of 120 sq. ft., and the following table gives the calculated yields per acre of the herbage and the analytical results:

	Commercial strains A		Grazing strains		Commercial strains B	
	%	Yield cwt.	%	Yield cwt.	%	Yield cwt.
Total crop	—	131·6	—	130·0	—	130·0
Moisture	77·50	—	77·40	—	77·50	—
Ether extract	0·81	1·07	0·83	1·08	0·85	1·17
Albuminoids	4·95	6·52	4·74	6·36	4·72	6·14
Crude fibre	4·20	5·53	4·05	5·27	4·12	5·36
Ash	2·05	2·70	2·10	2·73	2·09	2·72
Sol. carbohydrate	10·49	13·81	10·88	14·14	10·72	13·94
True protein	4·20	5·53	4·08	5·30	4·00	5·20

The results indicate that under the soil and climatic conditions prevailing there has been no superiority either in yield or analysis of the special grazing strains mixture over the ordinary commercial mixture. This is not in accordance with the results obtained by Stapledon (**6**) in many of his Welsh experiments (**7**), but it is in accordance with the experiences of Moore in Yorkshire (**8**), and of Findlay in the north of Scotland (**9**), and with the observations of most West of Scotland Agricultural Organizers and of other members of staff of the West of Scotland Agricultural College. At Morriston, as on numerous other Ayrshire farms, the most important grazing plant proved to be wild white clover, which thrives on soils well supplied with phosphate and potash and where the *p*H value of the soil is not too low. It is perhaps worth noting that the ordinary commercial rye grass is Ayrshire and the commercial timothy is Scotch, and that these strains being indigenous to west Scotland are likely to be at least as productive in Ayrshire as Aberystwyth-bred strains introduced into the area.

CARBELLO EXPERIMENTS, CUMNOCK

The importance of basic slag in producing higher crop yields and improved herbage has been demonstrated by results obtained by the writer on Carbello farm, north-east of Cumnock. Randomized plots were laid off for a swede manuring experiment in 1935, in order to test the availability and effects of high-soluble, medium-soluble, and low-soluble slags. Along with 1¼ cwt. sulphate of ammonia and 2½ cwt. potash salts per acre, the slags were applied at two rates, viz. to supply 56 and 112 lb. P_2O_5 respectively per acre. The proportions of the total contained P_2O_5 soluble in the standard citric acid solution were as follows: low soluble 24%; medium soluble A 44%; medium soluble B 53%; high soluble 89%. Yields of swedes in tons per acre were as follows:

	Control	Low	Medium A	Medium B	High	Limestone*	S.E.	*p*H
56 lb. P_2O_5	2·31	13·96	16·77	21·38	23·61	3·08	±1·13	5·2
112 lb. P_2O_5		20·05	20·37	24·50	25·24	4·39		

* Equivalent to CaO in slags (3½ and 7 cwt.).

It is obvious from the turnip yields that the medium soluble slags were different in type, A being little superior to the low soluble, and B being little inferior to the high soluble. The importance of a higher dressing when the solubility is low is demonstrated by the above results, where the difference in yield between the two rates of dressing is only 1·63 tons with the high-soluble slag, but is 6·09 tons with the low soluble.

The land was sown out to grass under an oat crop in 1936; hay was cut in 1937, and the land was grazed in 1938 and subsequent years. Even although a light dressing of mineral phosphate had been applied in 1938, the effects of the previous treatment on the sward was obvious, and in August 1941 botanical analyses were made and soil samples taken from the various control, limestone (equal to CaO content of 7 cwt. basic slag), low-soluble and high-soluble slag plots at both rates of dressing, equivalent to 56 and 112 lb. P_2O_5 per acre. The results were as follows (average of the plots under each treatment):

	Control	$CaCO_3$	Low 56	Low 112	High 56	High 112
Lolium perenne	9·7	13·0	15·3	18·3	17·7	20·0
Dactylis glomerata	1·0	0·3	2·3	1·3	4·0	3·7
Phleum pratense	—	—	0·3	—	1·0	2·0
Cynosurus cristatus	3·3	1·7	5·7	4·0	8·3	7·3
Poa trivialis	12·0	17·3	14·0	19·7	18·0	15·0
Trifolium repens	14·0	26·7	24·3	27·3	24·7	28·0
Holcus lanatus	21·7	19·3	20·3	17·3	14·3	15·7
Agrostis spp.	24·7	12·0	9·0	5·0	4·3	2·0
Bellis perennis	4·0	4·7	3·7	3·3	3·0	4·3
Ranunculus repens	5·3	4·3	4·0	3·0	3·7	2·0
Juncus effusus	4·3	0·7	1·0	0·7	1·0	—
Viz. Useful plants	40·0	59·0	62·0	70·7	73·7	76·0
Inferior plants	60·0	41·0	38·0	29·3	26·3	24·0
Soil *p*H	5·30	5·30	5·45	5·35	5·35	5·54

In spite of the *p*H figure being only slightly lower on the control plots, there was still a strong contrast between the swards resulting from the 1935 treatments. The useful plants on the control plots only average 40%, while on the high-soluble slag plots they approximate to 75%. There was still a greater difference between the two rates of application on the low-soluble than on the high-soluble slag plots. The few cwt. limestone per acre had a beneficial effect on the sward, though inferior to the slag dressings. No significant differences between plots were shown by the soil analyses; possibly due to removal of phosphate and lime by additional production.

In 1935 also in the same field a calculated manurial and lime requirement dressing deduced from the soil analysis and consisting of 6½ cwt. (27% P_2O_5) ground mineral phosphate, 2¾ cwt. potash salts, 2 cwt. nitrochalk and 9½ tons (85% $CaCO_3$) ground limestone, all per acre, was tested on the swede crop against the normal 10 cwt. per acre mixed manure employed in the district and analysing 3% nitrogen, 13% P_2O_5, and

3% K_2O. Growth was slow in the early stages with the special manurial dressing, probably owing to the very slow availability of mineral phosphate on a soil made neutral by an abnormally heavy limestone dressing. Growth improved later and the final yield was 19·9 tons per acre as compared with 22·5 tons with the ordinary manurial dressing. The oat crop in 1936, the hay crop in 1937, and the pasture in subsequent years were much superior as a result of the special treatment. In August 1941 botanical analyses and soil samples were taken on this plot and from the surrounding area, treated in the ordinary way in 1935 with ordinary turnip manure. Results were as follows:

	Special treatment	Ordinary manure
Lolium perenne	35	11
Dactylis glomerata	2	1
Phleum pratense	2	1
Cynosurus cristatus	8	3
Poa trivialis	11	12
Trifolium repens	33	30
Holcus lanatus	1	18
Agrostis spp.	2	15
Ranunculus repens	2	4
Bellis perennis	4	3
Juncus effusus	—	2
Viz. Useful plants	91	58
Inferior plants	9	42

	Soil	Subsoil	Soil	Subsoil
Soil *p*H	6·49	6·43	5·35	5·50
P_2O_5 mg. per 100 g. soil	13·4	6·4	11·0	5·4
K_2O mg. per 100 g. soil	Trace	Absent	Trace	Absent

The superiority of the sward is shown by the fact that only 9% inferior plants are present on the plot receiving its requirements in full against over 40% on the adjoining land. Growth also starts earlier in the spring and production is greater throughout the season. The *p*H value of the soil has fallen somewhat from the 7·0 figure obtained in 1935; a certain amount of loss of lime to the subsoil has taken place, as can be observed from the contrast between the two subsoil figures.

BRACKENHILL DEMONSTRATION AREA STUDIES, 1939–42

In view of the results obtained on the demonstration plots laid down at Brackenhill, Catrine, from 1936 till 1939 for the benefit of the local farmers, it was decided that further detailed studies on the sward for the next three years, and its relation to the lime status of the soil, should be made. At the commencement of the experiments the *p*H value of the soil to a depth of 9 in. was practically uniform, only varying very slightly from 5·0. One series had been sown out to grass with a second corn crop, the first oat crop in 1936 having been after pasture which had lain ten years. Part of the land received for both oat crops and for the 1938 hay crop, 'acid' manures in the form of sulphate of ammonia and superphosphate, and the remainder was dressed with 'basic' manures in the form of nitrochalk or calcium cyanamide and basic slag or mineral phosphate. Potash was applied in addition each year to all plots. In 1937 half of each section had received lime at the rate of 1½ tons CaO per acre. The liming gave a 5% increase in the oat yield on the 'acid' manure sections, and a 3% decrease on the 'basic' manure plots.

The second series was sown out to grass in 1938 with an oat crop, following swedes taken as the second crop of the rotation. Liming increased the oat yield by almost 5%

on the 'acid' manure sections, but caused a slight reduction (about 3%) on the basic manure sections. The hay crop under both treatments in 1939 was increased 14% by liming.

The land not devoted to a root crop was accordingly under first year's pasture in 1939, and the green-cropped area was first under pasture in 1940. The standard grass-seed mixture employed was composed of 20 lb. *Lolium perenne*, 6 lb. *Dactylis glomerata*, 4 lb. *Phleum pratense*, 6 lb. *Festuca pratensis*, 1 lb. *Cynosurus cristatus*, 1 lb. *Poa trivialis*, 2 lb. *Trifolium pratense*, 1 lb. *Trifolium hybridum*, and ¾ lb. *Trifolium repens*, all per acre.

Botanical analyses were made of the various treatment plots in the autumns of 1939, 1940, 1941 and 1942, and soil analyses were made in October 1939 and September 1942. Results were as follows:

A. *Non-green-cropped plots*

(Abbreviations used in the tables are: A = 'acid' manure; B = 'basic' manure; L = lime.)

	September 1939				September 1941				September 1942			
	A	AL	BL	B	A	AL	BL	B	A	AL	BL	B
Lolium perenne	11	22	32	20	10	20	25	19	10	23	31	21
Dactylis glomerata	6	4	6	6	2	2	9	5	1	3	3	2
Phleum pratense	2	5	9	4	—	2	3	1	1	2	2	1
Cynosurus cristatus	—	1	4	2	—	2	3	7	2	9	13	16
Poa trivialis	—	—	—	—	1	3	1	1	—	—	1	—
Trifolium pratense	2	6	5	6	—	—	—	—	—	—	—	—
T. repens	3	16	19	10	12	25	29	22	11	17	23	21
Holcus lanatus	30	22	9	19	25	24	15	24	25	23	14	17
Agrostis spp.	30	14	2	18	39	8	7	11	38	9	2	11
Anthoxanthum odoratum	—	—	1	2	—	—	—	—	—	—	—	—
Ranunculus repens	14	8	12	13	9	12	8	9	10	13	9	11
Prunella vulgaris	2	2	1	—	—	—	—	—	—	—	—	—
Bellis perennis	—	—	—	—	—	2	—	—	2	1	2	—
Hieracium spp.	—	—	—	—	2	—	—	1	—	—	—	—
Viz. Useful plants	24	54	75	48	25	54	70	55	25	54	73	61
Inferior plants	76	46	25	52	75	46	30	45	75	46	27	39
Soil pH: 0–3 in.	4·73	5·27	5·46	5·10	—	—	—	—	4·96	5·41	5·87	5·46
3–9 in.	4·90	4·99	5·18	4·95	—	—	—	—	5·13	5·30	5·58	5·28

From the above figures it is evident that the soil reaction due to the treatment during the rotation has greatly affected the constitution of the sward. As was to be expected, the higher the pH value of the soil, the higher the proportion of useful plants in the sward. The botanical analyses of the various sections altered little during the three years' observation period. In 1939 as a result of the 'acid manuring' during the rotation, the sward consisted of approximately three inferior plants to one useful plant; the 'basic manuring' followed by liming has reversed these figures to three useful for every inferior plant. 'Basic manuring' without lime has given approximately equal numbers of useful and inferior plants; a similar botanical analysis has resulted from 'acid manuring' plus liming. Changes have been negligible during the three years apart from a gradual improvement in the 'basic manure' unlimed section.

Chemical analyses were made of the herbage from the various sections in October 1939, and determinations made of the nitrogen, P_2O_5 and CaO contents. The results of the treatments averaged as follows (percentages of dry matter):

	A	AL	BL	B
Nitrogen	2·37	2·30	2·62	2·40
P_2O_5	0·638	0·538	0·684	0·773
CaO	0·726	1·169	1·685	1·120

The nitrogen content is slightly higher with the basic manure, with little difference between limed and unlimed sections. The phosphate content is rather higher in the herbage on the basic manure sections, the herbage on the unlimed portions of both basic and acid manuring areas having a rather higher P_2O_5 content than that on the limed portion. The CaO content is definitely highest in the herbage on the limed portion of the basic manure section, while it is lowest in the herbage on the unlimed portion of the acid manure section.

B. *Green-cropped land*

	October 1939				September 1940			
	A	AL	BL	B	A	AL	BL	B
Lolium perenne	29	40	41	37	9	22	28	20
Dactylis glomerata	19	12	11	10	10	19	15	19
Phleum pratense	9	13	14	12	7	18	14	9
Cynosurus cristatus	—	—	—	—	—	2	2	2
Poa trivialis	—	—	—	—	—	2	3	1
Trifolium pratense	1	11	15	11	1	4	9	7
T. hybridum	—	1	1	3	—	—	—	—
T. repens	—	3	5	5	1	6	9	13
Holcus lanatus	18	6	4	9	27	13	8	14
Agrostis spp.	12	3	—	2	32	3	1	4
Ranunculus repens	12	11	9	11	13	11	11	11
Viz. Useful plants	58	80	87	78	28	73	80	71
Inferior plants	42	20	13	22	72	27	20	29
Soil *p*H: 0–3 in.	4·93	5·44	5·80	5·39	—	—	—	—
3–9 in.	5·04	5·07	5·38	5·19	—	—	—	—

	September 1941				September 1942			
	A	AL	BL	B	A	AL	BL	B
Lolium perenne	10	18	24	20	12	27	30	21
Dactylis glomerata	6	14	12	8	3	4	6	1
Phleum pratense	—	7	3	2	1	1	2	2
Cynosurus cristatus	—	2	4	4	—	10	12	8
Poa trivialis	—	—	1	—	1	—	—	—
Trifolium pratense	—	—	1	1	—	—	—	—
T. repens	6	23	25	22	7	23	26	25
Holcus lanatus	28	13	14	19	20	18	11	22
Agrostis spp.	42	14	5	13	44	2	—	11
Ranunculus repens	8	9	10	10	11	9	10	9
Bellis perennis	—	—	1	1	1	6	3	1
Viz. Useful plants	22	64	70	57	24	65	76	57
Inferior plants	78	36	30	43	76	35	24	43
Soil *p*H: 0–3 in.	—	—	—	—	5·09	5·66	5·97	5·53
3–9 in.	—	—	—	—	5·06	5·31	5·61	5·46

The final results on these plots after three years in pasture are similar to those on the plots where the land was sown back to grass without the interposition of a root crop. While the cleaning of the land with a root crop resulted in fewer weeds being apparent in the first 18 months after the seeds were sown, deterioration took place later, chiefly on the land where neither slag nor lime had been applied during the rotation. By the end of a further 18 months the swards had become stabilized, the only difference from the non-green-cropped area being that the 'acid manure' section of the limed portion of the green-cropped, with a higher *p*H value, had fewer inferior plants, these being in the region of 35% of the sward.

On both green-cropped and non-green-cropped land only relatively slight benefit was obtained from using special grazing strains or additional quantities of rye-grass seed. In the following table the figure following the treatment symbol gives the number of lb.

of perennial rye grass used per acre in the mixture for which the botanical analysis appears immediately below:

	Green-cropped				Non-green-cropped				Green-cropped Commercial				Non-green-cropped Commercial			
	Commercial		Grazing		Commercial		Grazing		B	BL	B	BL	B	BL	B	BL
	A	AL	A	AL	A	AL	A	AL	20	20	30	30	20	20	30	30
Lolium perenne	12	27	12	37	10	23	13	28	21	30	25	36	21	31	30	35
Dactylis glomerata	3	4	3	1	1	3	3	3	1	6	1	2	2	3	3	3
Phleum pratense	1	1	5	4	1	2	2	2	2	2	2	1	1	2	1	1
Cynosurus cristatus	—	10	4	14	2	9	5	7	8	12	12	11	16	13	12	14
Poa trivialis	1	—	—	1	—	—	1	2	—	—	—	1	—	1	1	—
Trifolium repens	7	23	5	22	11	17	7	20	25	26	22	27	21	23	23	25
Holcus lanatus	20	18	18	10	25	23	24	20	22	11	19	10	17	14	16	12
Agrostis spp.	44	2	43	1	38	9	36	6	11	—	8	1	11	2	4	—
Ranunculus repens	11	9	10	9	10	13	8	12	9	10	11	5	11	9	10	10
Bellis perennis	1	6	—	1	2	1	1	—	1	3	—	6	—	2	—	—
Viz. Useful plants	24	65	29	79	25	54	31	62	57	76	62	78	61	73	70	78
Inferior plants	76	35	71	21	75	46	69	38	43	24	38	22	39	27	30	22

The foregoing tables show that, while on the average the sward from the grazing strains mixture contains 8% more useful plants and hence 8% fewer weeds, the improvement resulting from liming on these 'acid-manured' plots with both mixtures is several times greater, showing on the average an increase from 27% useful plants in the sward to 65%, and accordingly a reduction in weeds from 73 to 35%, the improvement being greatest on the land which had been previously cleaned with a root crop. The use of 30 lb. of perennial rye grass in the seeds mixture in place of 20 lb. has given a sward with 5% fewer weeds on the average, but even on the 'basic-manured' plots the difference due to liming averages 14%, an improvement almost three times greater.

The contrasts in appearance between the various treatments have become more marked with the passage of time, especially on the land which had been cleaned with a root crop during the rotation. The plots which had received only the commonly used manures for the various crops and hay (and consisting of superphosphate, sulphate of ammonia and potash salts) without a lime dressing at the end of the rotation were always very poor in colour, and being less palatable to the dairy cattle, were always rough, contrasting strongly with the areas where lime had been used in addition, or basic manures, such as slag, nitrochalk, etc., employed. There has always been comparatively little visible difference between the 'acid manure' plus lime and the 'basic manure' sections, both being equally well eaten and similar in colour and appearance. The 'basic manure' plus lime sections have been slightly superior in colour and have shown the greatest vigour of growth throughout the year. The quality of the pasture has accordingly been chiefly influenced by the manures (including lime) employed and their effects on the surface soil reaction. The higher the *p*H the lower the proportion of inferior plants.

DISCUSSION

In south-west Scotland the condition of rotation pastures is largely dependent on the soil reaction and the phosphate supply. On most intensively cropped lands there is generally a sufficient supply of phosphate, but in many cases in the past 20 years land has been laid down to grass, when seriously deficient in lime, with consequently unsatisfactory results. Using special grazing strains is not a solution for such conditions, and such strains have not generally shown, even under satisfactory conditions, any superiority to commercial rye grass or timothy. The raising of the soil lime-status is the only satisfactory method of obtaining superior pasture. Though the lime-status may be satisfactory for growing good arable crops such as potatoes and oats, it may often be too low for growing good pasture.

On less intensively cropped soils, where phosphate is seriously deficient as well as lime, liming will not in itself ensure lasting good results when reseeding land to grass. Under such circumstances basic slag during the rotation cropping has proved valuable, increasing the phosphate and obviating to a large extent the need for lime when sowing out. The conditions obtaining at Carbello and Brackenhill are typical of those on numerous upland dairy farms in south-west Scotland, where cropping should be directed to creating good conditions for the establishment of grass at the end of the cropping period. Methods adopted of securing such conditions and how they succeeded have been described. As lime and bases sink in the soil, such applications should be concentrated in the surface layers, in which establishment of the grass seeds takes place.

The influence of the grass-seed mixture has proved of much less importance in its effect on the botanical composition of the pasture, though it may affect the hay crop to some extent in the first year. Botanical differences in the sward thereafter are almost entirely due to the soil conditions. In that respect experiences in the west of Scotland differ somewhat from those in certain other parts of the country, where the seed mixture has apparently a considerable influence on the sward, and grazing strains prove superior to commercial strains (which may include Ayrshire perennial rye grass and Scotch timothy).

SUMMARY

The marked influence of lime, where arable crop yields were suffering seriously, on the yield of hay and the botanical composition of the sward on intensively cropped land in Ayrshire is described, as well as its influence on the grass seeds sown 14 years later.

The effect of lime on the sward on another Ayrshire cropping farm where the lime deficiency was less acute, and the limited effect of the composition of the seed mixture on its botanical analysis are also described.

The effects on the composition of the sward of 'acid' and 'basic' manures during the cropping rotation, with and without lime, are given in full for typical south-west Scotland dairy farms. How the rotation cropping and manuring can be made a good preparation for the pasture afterwards is indicated.

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OUTLINE OF THE VEGETATION IN WADI ARABA

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(*With one Figure in the Text*)

CONTENTS

	PAGE		PAGE
Introduction	204	Soils and vegetation . . .	206
Physiography	204	Summary	212
Geology	205	References	213
Climate	205		

INTRODUCTION

The purpose of this paper is to give a brief account of the plant communities of Wadi Araba in their relation to soil and other ecological factors. Wadi Araba (one of the least known deserts of the Nearer East) is a part of the Syro-African Rift Valley situated between the Dead Sea and the Red Sea (Gulf of Aqaba).

The first to cast some light on the botanical knowledge of Wadi Araba was H. C. Hart who in 1883–4 took part in a scientific expedition in this region led by the geologist E. Hull. The botanical results of this expedition were published in a comprehensive work entitled *Fauna and Flora of Sinai, Petra and Wadi Araba* (1891).

Unfortunately, Hart's investigations in Wadi Araba were limited to the southern and eastern part of the valley only, and even in these parts no attention was given either to the vegetation or to the ecological features of the valley. For instance, Hart does not make any mention of *Haloxylon persicum* which forms extensive 'Saxaul forests' in this valley. Similarly, Rost and Aaronsohn visited only the north-eastern sector of the valley.

It was not until December 1942 that we were first able to study and map the soil and vegetation units of nearly the entire area.

PHYSIOGRAPHY

Wadi Araba is a valley about 170 km. in length and 5–20 km. wide. It is bounded on the west by the mountains of the Zinn Desert (Far Negeb), averaging in height 600 m., on the east by the Edumean Mountains which attain an altitude of about 1750 m. The altitude of this valley varies from −396 m. (southern shore of the Dead Sea) to +240 m. (near Qaa el Saiydin, about 70 km. north of Aqaba). The watershed between the Dead Sea and the Red Sea is in the neighbourhood of Qaa el Saiydin.

Two main watercourses run the length of the valley: The one is Wadi Ghamar-Jeib, which empties into the Dead Sea, the other, Wadi Saeh, is lost in the sands on its way to the Gulf of Aqaba. Although these wadis are fed by numerous tributaries from the lateral mountain ranges, there is no permanent watercourse here due to the extreme aridity of the region.

Wadi Araba may be subdivided into three parts morphologically: (1) the Aqaba Valley, (2) the central Part, (3) the Ghor of the Dead Sea.

(1) The Aqaba Plain comprises the southern part of the valley, from the shores of the Gulf to the watershed, about 70 km. north of Aqaba. As its slope is slight and shifting sand dunes are present, the drainage of this part is seriously impeded, so that

three inundated flats known as Qaa el Deifieh, Sabkhat el Taba and Qaa el Saiydin are formed. These flats are surrounded on either side by dunes, sandfields or gravel land. The occurrence of a few saline springs in the border of these plains indicates the comparatively high-water table of the region.

(2) The central part of Wadi Araba. Here the valley is very broad and Wadi Jeib and Wadi Ghamar form broad beds covered by vegetation. Large areas of gravel land and sand dunes characterize this region, while the northern edge is covered by Diluvium Marls ('Lissan Marls'), broken up into hundreds of fissures and furrows ('broken land') and constituting absolute desert land.

(3) The Ghor of the Dead Sea is an extensive plain inundated by the latitudinal wadis, by Wadi Jeib and Wadi Quseib as well as by several springs mainly located at the periphery of this plain. A belt of considerable breadth is seasonally flooded by the Dead Sea waters. Almost the entire area is highly saline. Abundantly watered, densely covered by halophytic shrubs and trees, it constitutes the most vivid area of the valley. At the eastern margin of the area two fertile oases are located, Ghor es Safia (fed by Wadi Hasa) and Ghor el Feife (fed by Wadi Feife). These oases are the only centres of comparatively rich Sudano-Deccanian vegetation.

The hydrographical features of Wadi Araba are mainly responsible for the distribution of the salt marshes. While in the well-drained central part typical halophytic vegetation is of rare occurrence, halophytic vegetation is very abundant in the badly drained plains of the south and the richly watered plain of the Dead Sea Ghor.

GEOLOGY

Our principal source of information on the geology of this region is Hull (1885). Mention is made here of only such geological data as have direct bearing on the soil formation of the region. In the greater part of the valley the soil has been accumulated from the adjacent mountains.

Mountain ranges of igneous rocks consisting of granite, porphyry, etc., occur along almost the whole eastern and in the southern part of the western limit of the valley. These rocks weather to sandy soil.

The so-called Nubian Sandstone formations which occur here and there at the borders and especially in the western side of the Wadi belong mainly to the Lower Cretaceous. Its weathering product is a sandy soil hardly distinguishable from that originating from granite rocks.

The Upper Cretaceous is mainly represented by soft Senonian limestone, very abundant along the western border; it is the source of calcareous grey soils intermingled and covered with flint pebble.

In the northern part of the valley the Lissan Marls, a deposit of the Pleistocene southern prolongation of the Dead Sea, occupy vast stretches. Pleistocene and recent formations are the sand dunes, the gravel plains as well as the alluvial and halophytic soil of the northern and southern portions.

CLIMATE

No temperature data are available for this region and data on the annual amount of precipitation are very inadequate. According to Ashbel (1938) Wadi Araba is included within the isohyets of 25–50 mm. Since this amount of rainfall is not sufficient to support vegetation of any kind, vegetation is here controlled not by atmospheric but by soil moisture. The latter is decisively conditioned by topographical factors (depressions, wadis, etc.) and by the ground-water table level. The vegetation of Wadi Araba is accordingly limited mainly to plains and valleys. But here the constitution of the soil is a determinant factor on the character and composition of the vegetation.

The following rainfall figures for this region were obtained from the meteorological station of Sodom (southern shores of Dead Sea) and Themed (60 km. west of Aqaba (Ashbel, 1938).

Themed			Sodom		
Year	Annual amount mm.	Rain days	Year	Annual amount mm.	Rain days
1921–2	25·5	7	1934–5	29·4	7
1922–3	14·5	5	1935–6	49·9	16
1923–4	9·0	9	1936–7	18·8	8
1924–5	39·5	10	1937–8	49·0	17
1925–6	313·0	13	1938–9	—	—

These figures indicate not only the small quantity of rain but also its erratic character.

The phytogeographical position of Wadi Araba

According to Eig (1938), Palestine is subdivided into three plant geographical territories: the Mediterranean, the Irano-Turanian and the Saharo-Sindian. The last is also a district of penetration of the Sudano-Deccanian element in Palestine. The whole of Wadi Araba is within the Saharo-Sindian region. Were it not for the additional moisture Wadi Araba obtains from the watercourses emptying into it, the whole region would constitute a bare desert. As it is, however, this region boasts a comparatively rich vegetation. Besides typical Saharo-Sindian desert plant communities which inhabit the greater part of the valley, the halophytic vegetation occupies considerable areas and in the north-eastern part savannah plant communities also occur.

SOILS AND VEGETATION

One of the most striking features of Wadi Araba vegetation is the close relation between plant communities and soil varieties. The following is a description of the principal soil varieties met with in this region and the plant communities thereto confined.

The soils of Wadi Araba may be subdivided into six varieties* according to chemical and mechanical constitution. These are: (1) sand dunes and sand plains, (2) Hammadas, (3) Lissan Marl soil, (4) calcareous-loess soils, (5) saline marshes, (6) alluvial soils of Sudano-Deccanian oases.

(1) *Sand dunes and sand plains*

These soils occupy almost one-fourth of the whole valley. Granite rock and Nubian Sandstone are the parent material of this soil. Sand fields are considerably commoner than dunes. The following figures may illustrate the composition of this soil. For the sake of brevity the figures for one typical soil sample only are reported here and later. $CaCO_3$ was calculated from CO_2; percentage refers to dry matter.

Sands south of Qaa el Saiydin (Magazanik, 1933):

Depth cm.	Soluble salts %	Cl %	$CaCO_3$ %	Coarse and fine sand %	Silt %	Clay %
50–100	0·65	0·079	10·36	—	—	—
100–150	0·52	0·062	—	85·67	11·87	2·76

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* The term variety is applied here in a general sense and not as a definite typological unit.

Other samples taken from sands between Qaa el Deifieh and Sabkhat Taba are more or less similar in composition. The sand dunes may thus be regarded as calcareous and as free from injurious high concentrations of chlorides.

Vegetationally this soil type is characterized by *Haloxylonetum persicae* which is one of the most abundant and most typical plant communities of this valley. The composition of this plant community is as yet inadequately studied. During the season we visited Wadi Araba (December) the following plants were noted: *Haloxylon persicum* (3–3), *Calligonum comosum* (1–2), *Salsola foetida* (1–3), and *Plantago cylindrica* (+–1). The general degree of coverage is about 40% here. The figures following the plant names indicate coverage (first figure) and sociability (second figure) according to the Zürich-Montpellier scale.

Haloxylon persicum is a tall shrub or a tree reaching 4 m. in height. It is the well-known 'Ghada' of the Arabs and is used here for charcoal and for camel fodder. It is also encountered in Wadi Ithm (Edom), and is especially common in the Arabian Nefud. It is this species which constitutes a main component of the Central Asian 'Saxaul forests'.

(2) *Hammadas*

Hammada is a general and conventional term for gravelly desert plains. In Palestine, Sinai and the Syrian Desert, Hammada deserts are the commonest desert type. These are slightly rolling plains, the soil of which is mostly gypseous or highly calcareous, sometimes also sandy. The main feature of this soil is the great quantity of pebble and gravel of differing size and constitution covering the surface and forming the principal part of the soil in the upper horizons. In the deserts of Palestine and the neighbouring countries Hammadas represent the most sterile soils. They are mostly limited to a region obtaining less than 100 mm. of annual rainfall, and therefore almost deprived of a vegetation cover. The only refuges of a more or less dense vegetation in such areas are the broad wadis or depressions which enjoy greater moisture. Hammada is to be regarded as a zonal soil type conditioned by the feeble chemical weathering on the one hand and the prevailing winds on the other. Unprotected by vegetational cover, the finer surface soil particles are blown off with the deflating action of wind storms. Over half of the soils of Wadi Araba belong to the Hammada type. The following may serve an example of the composition of the Hammada soil in this region:

Hammada soils south of Ghor el Ajram

Depth of soil ...	20 cm.	50 cm.	Depth of soil ...	20 cm.	50 cm.
H_2O (105° C.) (%)	2·1	1·6	Clay (%)	2·5	5·0
Coarse sand (%)	30·1	39·3	$CaCO_3$ (%)	12·5	5·1
Fine sand (%)	52·8	40·0	Soluble salts (%)	1·49	1·09
Silt (%)	—	—	Cl (%)	0·517	0·616

In other more typical samples from Wadi Jerafi and Ghor el Ajram the quantity of soluble salts did not exceed 0·2% and that of Cl 0·06%. On the other hand, one sample from sterile lands north of Qaa el Saiydin contained 4·11% of soluble salts. From these figures as well as from our observations in other Hammada deserts, it is obvious that the Hammada in its typical constitution is generally a 'non-saline' soil. The sterility of Hammadas is thus a result of drought and mechanical composition and not of chemical composition. In Wadi Araba three edaphically and vegetationally well-defined varieties of this soil type were observed.

(1) Typical Hammada as represented in Ghor el Ajram is inhabited by Anabasidetum articulatae. This plant community is the most typical expression of the Hammada not only in Wadi Araba but also in the Syrian Desert, Sinai and southern Transjordan. The most characteristic components of this plant association, as obtained from several records made in the region, are *Anabasis articulata*, *Salsola rigida* var. *villosa*, *Traganum nudatum*, *Zygophyllum dumosum*, *Asteriscus graveolens*, *Asteriscus pygmaeus*, *Anastatica hierochuntica*, *Aerva tomentosa*, *Ochradenus baccatus*, *Panicum turgidum*, *Fagonia* sp. Owing to the late season few annuals were found. In general the coverage rarely exceeds 5%; often it is less than 2%, *Anabasis articulata* is, however, always dominant.

(2) A rather common variety of the aforementioned soil is that Hammada confined to shallow wadis and depressions or to plains at the foot of elevations. Here the soil is more silty and contains sufficient moisture to permit the entry of non-halophytic trees. The Anabasidetum articulati Acacietosum is the most characteristic plant association. It has a savannah-like appearance, the components of the Anabasidetum forming the lower stratum, *Acacia Raddiana* (= *A. tortilis*) and *A. spirocarpa* (sparsely scattered) the upper.

(3) The third variety may be termed 'sandy Hammada'. These are plains with a more or less shallow sand cover overlaying gravelly ground. The sand is intermingled with and loosely covered by much gravel, mainly of granite. Here the dominating plant association is Haloxylonetum salicornici, an association not adequately studied by us. It contains most species of the typical Anabasideum, but *Haloxylon salicornicum* is dominant. The latter is a rather psammophytic species resembling *Anabasis* in its external appearance.

(3) *Lissan Marl soils*

South of the Dead Sea Ghor and partly also west and east of it, immense stretches are covered by a white greyish calcareous ground which may hardly be termed soil, since it is barely distinguishable from the soft underlying rock. It contains a large amount of gypsum and soluble salts and may be regarded as an automorphous saline in contrast to the hydromorphous salines to be dealt with below. But it is not the salinity of the soil which is the decisive factor upon plant life here but the extreme drought. Markedly higher than the surrounding plains and wadis, it obtains its moisture from rains only and is therefore unable to support vegetation. Over the whole area cut by fissures and furrows not a single plant was found by us.

Quite different conditions prevail in the broad wadis (Wadi Jeib, Wadi Quseib) crossing this 'Bad land'. Here salts are leached out by the water running in winter, and sufficient moisture is retained for summer so that comparatively rich vegetation occurs here. Here are the figures obtained from a single soil sample from the bed of Wadi Quseib at a depth of 20 cm.:

	%		%
H_2O (105° C.)	1·2	Clay	1·25
Coarse sand	24·0	$CaCO_3$	33·9
Fine sand	39·0	Soluble salts	0·37
Silt	—	Cl	0·0258

In these non-saline moist wadi beds the dominating plant community is *Tamarix maris mortui-Calligonum comosum* association. The degree of covering does not exceed 5%. Its components are *Tamarix maris mortui* Guttm., *Calligonum comosum*, *Atriplex halimus*, *Lycium* sp., *Salsola tetrandra*, *Anvillea garcini*, *Zilla spinosa*, *Aerva tomentosa*.

The same plant association was also observed in Wadi Jerafi and Wadi Ghamar, but in the latter area *Haloxylon persicum* accompanies this association on sandy beds and the above-mentioned acacia trees are present on gravelly beds. The tamarix appears to be mainly *T. maris mortui* in this case also.

(4) *Calcareous-loess soil*

In its composition it strongly resembles loess but approaches the grey calcareous steppe soil of the other arid parts of Palestine. A sample taken from a depth of 20 cm. shows the following composition:

	%		%
H_2O (105°C.)	2·3	Clay	—
Coarse sand	0·6	$CaCO_3$	24·6
Fine sand	56·25	Soluble salts	0·24
Silt	16·25	Cl	0·023

Qaa el Saiydin is a flat plain watered by the wadis of the adjacent hills and adequately drained. It is the only cultivated soil found in the central part of the Araba. No remains of natural vegetation were found here except for scattered groups of *Salsola foetida* which seem, however, to be secondary here.

(5) *Saline marshes*

These soils, although heterogeneous in their chemical and mechanical composition, may be differentiated from the above-mentioned varieties by the comparatively high content of salts and by permanent or seasonal inundation. The salines of Wadi Araba are distinguished by their comparatively dense arboreal vegetation. They are mainly limited to the northern and southern sectors of the region. They are Solontchakes in composition, and the dominating salt is sodium chloride. The following units may be tentatively distinguished:

(1) The salt marshes of the southern sector. These salines consist of two flats separated from one another by sand dunes and sand fields. Between them two minor saline areas are intercalated. In the rainy season these flats are inundated by the ephemeral water-course and springs of their neighbourhood. The main obstacle impeding drainage are the shifting sands adjacent. The soil consists of sand and sandy clay. The upper layer of the soil dries up in summer and small hillocks accumulate through the action of the wind. The content of soluble salts varies from 17 to 2% and decreases generally with the depth. The reaction of the soil is slightly alkaline. The following figures were obtained from a soil sample taken in Sabkhat Taba:

Depth of soil ...	20 cm.	50 cm.	Depth of soil ...	20 cm.	50 cm.
H_2O (105°C.) (%)	6·1	3·9	Clay (%)	2·5	2·5
Coarse sand (%)	56·4	14·1	$CaCO_3$ (%)	6·2	8·6
Fine sand (%)	28·8	70·9	Soluble salts (%)	6·50	2·59
Silt (%)	—	—	Cl (%)	—	1·007

The reason for the great fluctuation in salt content may be purely topographical. The centre of the marshes is altogether free of vegetation and seems to be more saline than the periphery. The vegetation of these sandy marshes consists of two main plant associations: Suaedetum monoicae and Nitrarietum retusae.

The former covers the whole area between the Gulf of Aqaba and Qaa el Deifieh, and occurs also in the northern part of the Dead Sea Ghor. The degree of coverage is generally 40–50%. The following species were noted in this association: *Suaeda monoica* (3–3), *Cressa cretica* (+–1) and *Tamarix tetragyna* (+–3). The latter is a hydrohalophytic species limited chiefly to the interior parts of the saline. In the Dead Sea region Suaedetum monoicae contains also *Tamarix maris mortui* and single specimens of *Haloxylon persicum*.

Nitrarietum retusae is limited to Qaa el Deifieh about 10 km. north of Aqaba. The average degree of coverage does not exceed 10%. The following species were noted here: *Nitraria retusa* (1–3), *Tamarix tetragyna* (+–3), *Salsola* sp. (+–2), and *Suaeda vermiculata* (+–2). Mention should be made of groups of *Phoenix dactylifera* found within the saline area and a group of *Hyphaene thebaica* occurring in the periphery of this salt marsh. This is the northernmost station of this Sudano-Deccanian palm.

Apart from Qaa el Deifieh Nitrarietum occupies almost the whole area of Sabkhat Taba. Here, however, fragments of another association, Eragrostidetum bipinnatae, inhabit the outer zone of the flat. It is strange to find here the leading plant of the *Eragrostis bipinnata-Centaurea procurrens* association, so common in and characteristic of non-saline sandy clay soils of the Mediterranean coastal plain in Palestine. Does this plant, *Eragrostis*, exhibit so wide a range of ecological requirement, or does it behave here in the same manner as the non-halophytic *Prosopis farcata* behaves in the salines of the Dead Sea region? The latter sends its long rootstocks and roots into deep soil layers (up to 12 m. and more) where fresh water is supposedly available. Further investigations are required for the solution of this question. Patches of Eragrostidetum bipinnatae are also met with in the periphery of Dead Sea Ghor.

The edaphical differences between the habitats of Suaedetum monoicae and that of Nitrarietum retusae have not yet been distinguished.

(2) The salines of the Dead Sea Ghor. The whole area stretching from the shores of the Dead Sea to the northern border of the Lissan Marl formation consists of an extreme somewhat muddy marsh fed by salty and brackish water of the springs and wadis. The vicinity of the Dead Sea has an additional effect on the salinity of this area at least in the flooding zone of the sea. The soil is calcareous for the most part. A soil sample from near Ein Beda showed the following constituents: $CaCO_3$, 31·6%; H_2O (105° C.), 10·5%; soluble salts, 4·738% (at a depth of 20 cm.) and 2·00% (at a depth of 50 cm.). In another soil sample of this area the soluble salt content reached up to 20%.

In its edaphical constitution, namely, in the concentration of chlorides, the moisture and organic matter content of this area is very heterogeneous. At least three complex habitats may be distinguished, the one consisting of soils exhibiting permanently free surface water such as springs, brooks, etc., the second is limited to the margin of the Ghor near the foot of the Broken Plateau escarpments, where moisture is discharged into the plain from the hill sides mainly through lateral percolation, and inundation occurs only occasionally; the third habitat is the northern and central part of the Ghor where the soil is almost permanently inundated by a net of wadis and rivulets crossing the area on their way to the Dead Sea.

These three habitats constitute three hydrophytic regimes, each with its own mode of zonal arrangement of vegetation. At first glance it is not easy to ascertain the right lines for spatial delimitation of these three habitats on account of topographical disturbances. This proves possible, however, after careful examination of the vegetation. The main vegetation units of three habitats mentioned are:

(*a*) Saline or brackish springs and brooks, e.g. Ein Arus, Ein Beda, Ein Jeib, Ein

Quseib, Ein Hunsir, etc. The soil of the banks and the flooded zone is mostly a kind of peat formed under hydrohalopedic conditions. The vegetation is made up of three or four bands. Typically the banks are inhabited by a narrow band of *Phragmites communis* (as a pure stand) which is sometimes accompanied by *Typha* (*angustata*?) or *Cyperus distachyus*. Behind this there lies a broader belt of *Juncus arabicus* (= *J. maritimus* var. *arabicus*). Here are sometimes found also *Erianthus strictus*, *Inula crithmoides*, *Sonchus maritimus*, etc. The outer zone comprises a belt of *Aeluropus littoralis*. Very often a fourth belt of *Tamarix maris mortui* occurs. Not always are all bands represented, and topographical factors may account for the occasional non-appearance of one or more of the above belts.

(*b*) The hill-foot area. It is the driest area of the Ghor. The soil is grey and very calcareous. The vegetation is arranged in not always well-defined belts, depending on the topography of the surface. The lowest ground is occupied by Suaedetum monoicae intermingled with *Tamarix maris mortui* penetrating from the broad outlets of Wadi Jeib and Wadi Quseib and perhaps also from the fourth belt of the salt spring vegetation. Sometimes erratic specimens of *Haloxylon persicum* are also met with here. The second very striking belt is that of Eragrostidetum bipinnatae, occupying a land strip above the former. *Prosopis farcata*, *Alhagi maurorum* are often included in this belt. A still more elevated strip (lower zone of the hill slope) is inhabited by Nitrarietum retusae which is often fragmentary. These three bands are to be found not only at the southern edge of the Ghor but also at its western and eastern margin.

(*c*) The central and northern inundated area. The soil is calcareous, muddy and watered during almost the whole year. Vegetation appears here in more or less well-delimited belts parallel to the southern shoreline of the Dead Sea. In the north there is a very broad belt, the flooded zone of the Dead Sea, which constitutes a mud flat altogether bare of vegetation on account of the very high salt content. The next belt is occupied by *Arthrocnemum glaucum* which forms a rather dense and pure stand. The third belt towards the interior is of considerable width and consists of a mixed stand of *Arthrocnemum glaucum* and *Tamarix tetragyna*. It has a savannah-like appearance, the lower stratum being densely covered by *Arthrocnemum* while the upper is formed by more or less equally scattered trees of *Tamarix*. The third belt is formed by a stand of *Tamarix tetragyna* intermingled with *Tamarix maris mortui*. Although the belt of *Arthrocnemum-Tamarix* constitutes a transitional belt from the zonational point of view, it should be regarded as the main phytosociological unit of the habitat in question and as such was noted in the accompanying map.

Fig. 1 gives three transects through the halophytic vegetational complex of Dead Sea Ghor.

(6) *Alluvial oasis soils*

These are non-saline soils with high moisture content. They occupy outlet regions of fresh-water courses, and are rather well drained. Ghor es Safie and Ghor el Feife, situated at the north-east corner of the valley, are the main oases of Wadi Araba. The soils are not homogeneous in composition. Some are calcareous, others sandy. Owing to the comparatively high winter temperatures prevailing in this region and the abundance of soil moisture, a Sudano-Deccanian flora and vegetation has been able to develop. This comprises a few arboreal plant association, the most important of which is the *Zizyphus spina christi-Balanites aegyptiaca* association. Mention may be made of other Sudano-

Deccanian trees and shrubs occurring in these and in other poorly defined associations as follows: *Salvadora persica, Moringa aptera, Maerua crassifolia, Capparis decidua. Abutilon fruticosum, Abutilon muticum, Callotropis procera, Cordia gharaf, Solanum incanum, Tephrosia appollinea*, etc.

At present the primary vegetation is seriously affected by man who has turned these enclaves to oases with very primitive agriculture. Northwards other such enclaves are scattered around the Dead Sea and along the Lower Jordan Valley (Ein Gedi, Jericho, Ghor el Auja, Ghor Fara, etc.).

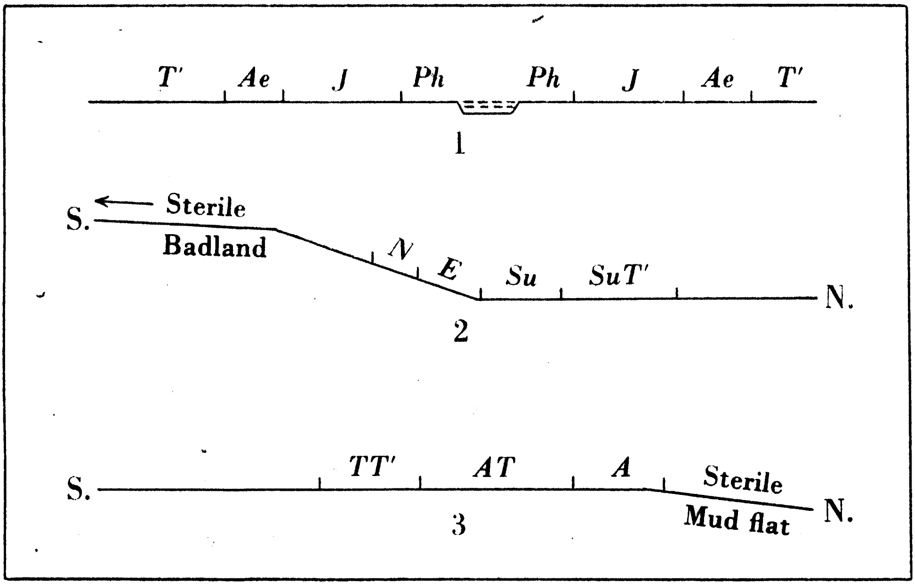

Fig. 1. Schematical transections through the vegetation belts of the Dead Sea Ghor. 1. Salt-water brook: *Ph, Phragmites communis*; *J, Juncus arabicus*; *Ae, Aeluropus littoralis*; *T', Tamarix maris mortui*. 2. Hill-foot area: *N, Nitraria retusa*; *E, Eragrostis bipinnata*; *Su, Suaeda monoica*; *T', Tamarix maris mortui*. 3. Central and northern area: sterile belt flooded by the Dead Sea; *A, Arthrocnemum glaucum*; *T, Tamarix tetragyna*; *T', Tamarix maris mortui*.

SUMMARY

1. The vegetation of Wadi Araba, a valley between the Dead Sea and the Red Sea, is herein described. This valley is remarkable for its abundant vegetation in comparison to other desert areas of similar climatical character.

2. Six different types of soil were found in this region, each with its own vegetation unit.

3. A preliminary account of the relations between soil and vegetation is given.

4. The mechanical composition, the salt and the water content of the soil have proved decisive factors on the character and composition of the vegetation.

5. The accompanying sketch map of vegetation and soils is a first attempt to provide cartographical information on the vegetation of the Nearer East.

6. The observations made on the comparatively rich halophytic vegetation may serve

as a basis for future detailed ecological and phytosociological studies of this vegetation here as well as in other districts of the Dead Sea region and the Jordan Valley.

7. The occurrence of large areas inhabited by the well-known Central Asian 'Saxaul forests' in the vicinity of the Red Sea is of great interest from the plant geographical and practical point of view.

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REVIEW

Erdtman, G. *An Introduction to Pollen Analysis.* 239 pp., 15 text-figs. and 31 plates. Chronica Botanica Co., Waltham, Mass., U.S.A.; Wm. Dawson and Sons Ltd., London, W. 1.

Dr Erdtman's book will be welcomed by pollen analysts and will do much to win wider recognition for pollen analysis as an established branch of science. It presents the basic technique of pollen analysis, standardized but still capable of extension and refinement, with critical consideration of its potentialities and limitations. The Editor's Preface describes the book as 'a short introduction to the principles of pollen analysis and an atlas of the principal types of pollen grain met by the beginning "pollen analyst"'. It is thus primarily a technical manual and not a survey of results.

After a brief historical introduction comes a chapter on the Chemistry of Peat, contributed by Dr H. Erdtman, who has skilfully seized a few bright strands from the dark and confused tangle that faces the investigator of 'humic acids'. Thus, for instance, evidence is referred to which suggests that the characteristic darkening of peat on changing from reducing to oxidizing conditions should be attributed to the presence of a quinoid grouping in 'humic acids', and this aromatic structure is explained on the supposition that lignin, 'a polymer of phenolic units containing methoxyl groups', is the main precursor of the acids in question. The author leans to the view that the acidity should be ascribed to the groupings found in hydroxyquinones rather than to the presence of carboxyl groups. A summary is also given of the recent researches of Zetzche and his colleagues on a highly unsaturated substance named Sporonine which has been found in varying proportions in the spore coats of *Lycopodium* and a few other types which have been investigated.

Dr G. Erdtman then continues and deals with methods of treating samples of pollen from various sources. The principal procedures described are the acetolysis method for fresh and herbarium material and the alkali and acetolysis-chlorination methods for subfossil material. These and others are described with a most acceptable wealth of practical detail.

The following six chapters fill half the book and give descriptions and illustrations of pollen grains and spores of vascular plants. Critical discussions are included here and there where there has been doubt or dispute as to the preservation of some type in peat or as to the interpretation of its occurrence in fossil strata. This section will be invaluable to the novice. One may feel slightly less certain that it will greatly help the rather more experienced worker in identifying grains that he does not know, because of the poor artistic quality of the illustrations; some of them may not be sufficiently life-like to fulfil the author's purpose, which was merely to 'convey suggestions as to the identification of pollen grains'. Under present conditions, however, it is perhaps churlish to sigh for the achievement of a higher standard, an achievement which would have demanded much time and great labour.

The rest of the book deals with a number of separate topics, among which may be mentioned pollen productivity and atmospheric pollen content. The pollen of Tertiary deposits is briefly discussed and the main pollen analytical literature is classified geographically. Most interesting of all is the chapter on surface samples, since it bears on the general problem of the interpretation of pollen diagrams. Varied examples are given, and some from Sweden suggest that there is a broad agreement between the forest composition and the pollen spectrum recorded in the surface layers of a region. Other examples, however, show no such agreement, and evidently caution is needed at present in drawing conclusions as to the actual plant communities which are represented by the pollen spectrum at any particular level in a deposit. There is good hope that this caution may be increasingly unnecessary as enough data accumulates to give the 'pollen picture' of a wide variety of present-day communities. Dr Erdtman describes ways of getting these 'pollen pictures' even when peat is not being formed, and widespread research along these lines might well give data of great importance in interpreting the historical record.

This is only one example of the way in which this book should stimulate new research as well as help in the doing of it, and we owe much to the author and his publishers in producing such an interesting and useful volume.

V. M. Conway

BIOLOGICAL FLORA OF THE BRITISH ISLES

L.C. (Ed. 11) Nos. **369–370**

ACER L.

E. W. JONES

A genus of shrubs and trees found throughout Europe, Asia (including North Africa), and North America and extending into mountains of the East Indies region. Leaves decussate, usually ± palmately lobed. Flowers in terminal cymes, small, inconspicuous, producing nectar, K5, C5, or absent, A8–10, carpels normally 2, but usually a small proportion 3, or rarely 4 or more. Fruit indehiscent, but separating into two (normally) single-seeded winged samaras. Sometimes a small proportion of the fruit are two-seeded. The flowers are of two kinds: (*a*) male, the gynaecium being abortive; (*b*) hermaphrodite, but functionally female, as the anthers do not open. Both kinds of flower are borne in the same raceme, but the proportions of each vary greatly from tree to tree.

Wood diffuse-porous; in transverse section vessels not distinctly visible to naked eye, but readily so with hand lens, *well separated* and *evenly distributed*, with little variation in size throughout ring; rays about as wide or a little wider than the vessels (but not twice as wide—cf. *Platanus*). Annual ring bounded by a pale line; little contrast between early and late wood (Chalk & Rendle, 1929). The following features are characteristic of anatomy of wood of *Acer*:

(*a*) The rays are homogeneous, and in tangential section of stem appear as 3–5 rows of uniform iso-diametric rounded thick-walled cells. All the cells are radially elongated.

(*b*) The vessels have spiral lines, and perforations in end walls are simple.

The wood of *A. campestre* closely resembles that of *A. pseudo-platanus* but is a little darker (*A. pseudo-platanus*, very pale brown to yellowish white; *A. campestre* pale brown), denser and smaller-celled (L. Chalk).

Only *A. campestre* is indigenous to Britain, *A. pseudo-platanus* being an introduced tree of long standing now fully naturalized, and *A. platanoides* a more recent introduction now in course of naturalization. These trees represent the following sections of the genus (Pax, 1902):

Section SPICATA. Leaves usually 3–7 lobed, lobes lobulate or serrate. Flowers in long corymbose raceme. Disk thick, extrastaminal. Fruit convex, wall strongly veined, not hard. *A. pseudo-platanus* L.

Section CAMPESTRIA. Leaves usually 3–7 lobed, lobes obtuse. Flowers in short corymbs. Disk thick, stamens inserted near its inner margin. Loculus of ovary hard-walled, wall strongly veined. *A. campestre* L.

Section PLATANOIDEA. Leaves 3–7 lobed, coarsely sinuate-dentate. Disk thick, stamens inserted in middle. Fruit flattened, with leathery weakly veined wall. *A. platanoides* L.

The basic chromosome number for the genus is 13 (Foster, 1933).

Morphology of A. pseudo-platanus *and* A. campestre

In the hermaphrodite flowers the anthers and pollen are apparently fully developed but the anthers do not open, and the filaments are about half the length of those in the male flower.

On the vigorously growing shoots of young or middle-aged trees there is a sharp differentiation into long shoots and lateral short spurs. The flowers are produced mainly from the terminal buds of the spurs. After the bud opens the axis elongates and usually produces one or two pairs of leaves below the inflorescence. The spurs do not usually flower until they are two years old, and often not until three years; occasionally one may flower two years in succession, but usually they flower in alternate years. A few of the terminal buds of long shoots often flower. As the tree ages all shoots take on the spur-like nature and branching of the twigs becomes largely dichotomous.

INSECTS AND FUNGI ASSOCIATED WITH *ACER*

FUNGI

p = *A. pseudo-platanus; c* = *A. campestre.*

ASCOMYCETES

ERYSIPHALES: *Uncinula aceris* Sacc., *p* and *c*.

SPHAERIALES: *Diaporthe niesslii* Sacc., *p*; *D. pustulata* (Desm.) Sacc., *p*; *D. varians* (Currey) Sacc., *c*; *Giugnardia acerifera* (Cooke) Lindau, *c*; *Eutypa scabrosa* Fuckel, *c*; *Mycosphaerella latebrosa* (Cooke) Schroet., *p*; *Calospora platanoides* Niessl., *p*; *Cucurbitaria homalea* (Fr.) Sacc., *p*; *Melanconia aceris* Phill. & Plowr., *p*.

HELOTIALES: *Mollisia petiolaris* Sacc., *p*.

PHACIDIALES: *Rhytisma acerinum* Fr., *p* and *c*; *Rh. punctatum* Fr., *p* and *c*.

BASIDIOMYCETES

AGARICALES: *Corticium anthochrous* (Pers.) Fr., *p*.

FUNGI IMPERFECTI

MONILIALES: *Cristulariella depraedens* (Cooke) von Höhnel, *p*; *Dactylosporium brevipes* Grove, *p*.

SPHAEROPSIDALES: *Phyllosticta platanoides* Sacc., *p*; *Ph. aceris* Sacc., *c*; *Aposphaeria inophila* Cooke, *c*; *A. i.* var. *pseudoplatani* Grove, *p*; *Asteroma aceris* Rab. & Desm., *c*; *Phomopsis platanoides* Died., *p*; *Ph. pustulata* Died., *p*; *Cytospora ambiens* Sacc., *p*; *Phleospora aceris* Sacc., *p*; *Ph. pseudoplatani* Bub., *p*; *Cytosporina nothi* Died., *p*; *Corynium pulvinatum* N. & S., *p*; *Leptothyrium acerinum* Corda, *c* and *p*; *L. platanoidis* Pass. apud Brun., *p*; *Diplodia subtecta* Fr., *c*; *D. acerina* Cooke & Mass., *c*; *Pseudodiplodia corticis* Grove, *p*; *Septomyza tulasnei* von Höhnel, *p*; *Callonema papillatum* Grove, *p*.

The great majority of the Fungi mentioned are harmless saprophyes, but *Uncinula aceris* and *Rhytisma acerinum* can cause considerable damage at times to *A. pseudoplatanus*. *Rhytisma* is almost invariably present on sycamore, but is absent in the smoky neighbourhood of Manchester (T. G. Tutin), Newcastle (G. L. Drury), Birmingham, etc. Watt believes that it may be largely the cause of slow growth of seedlings in shade. It is rare on *A. campestre*; *Uncinula* is perhaps the commonest fungus on this host. Among the Fungi not confined to *Acer* but causing damage to these hosts may be cited *Polyporus squamosus* (Huds.) Fr., causing heart rot of sycamore, and *Phytophthora cactorum* Leb. & Cohn. (= *P. omnivora* de Bary), causing death of seedlings. Damage to sycamore by *Nectria cinnabarina* (Fr.) Fr. may be seen on badly pruned street trees, but otherwise this fungus has but slight importance.

The above lists have largely been compiled by Dr A. Smith. Lists by Hegi (Fl. **5**), and Hempel & Wilhelm (1889) have been used, as well as the standard mycological works. W. R. Day has also supplied information.

INSECTS AND MITES (O. W. RICHARDS)

c = *Acer campestre*; p = *A. pseudo-platanus*; pl = *A. platanoides*; n = *A. negundo*.

The following list includes only those species closely associated with *Acer*, not those more commonly found on other plants. They have all been observed in Great Britain, though Continental records have been used in confirmation of the habits. The British distribution is given where sufficiently well known. Nomenclature of the Macrolepidoptera follows that of South (1939).

HEMIPTERA-HOMOPTERA

APHIDIDAE: *Myzus gracilis* Buckt., *p*; *Drepanosiphum platanoides* (Schrank), *c*, *p*, *pl*, widespread in Britain, common, and the important producer of honeydew; *D. acerina* (Walk.), *c*, *p*, south-east England; *Periphyllus testudinatus* (Thornton), *c*, *p*, *pl*, *n*, rarely on *Ribes rubrum*, widespread and common in Great Britain; *P. aceris* (Koch), *c*, *p*, southern England, not common; *P. lyropictus* (Kessler), *c*, *p*, rare; *P. horridus* Theob., *p*, Somerset; *P. templi* H.R.L., *c*, Kent (Ris Lambers, 1935); *Aphis aceriella* Theob., *c*, Herts.

ALEYRODIDAE: *Aleurochiton acerum* Kirk. (*aceris* auct.), *pl*, *p*, widespread in England but not common (Laing, MS.).

PSYLLIDAE: *Rhinocola aceris* (L.), *c*, widespread in southern England.

TYPHLOCYBIDAE: *Typhlocyba callosa* Then., *p*, also hawthorn and alder; *T. lethierryi* Edw., *c*, also horse chestnut; *T. nigriloba* Edw., *p*; *Eupteryx loewi* Then., *p*; *Alebra wahlbergi* (Boh.), *c*; also on many other trees.

BYTHOSCOPIDAE: *Idiocerus tibialis* Fieb., Kent, on *Acer* spp. on Continent.

HEMIPTERA-HETEROPTERA

CAPSIDAE: *Lygus viridis* (Fall.), *p* (China MS.); also on other trees, widespread in Britain.

LEPIDOPTERA

NEPTICULIDAE: *Nepticula decentella* H.-S., *p*, mines the seed vessels, Surrey and Sussex (Adkin, 1933); *N. sericopeza* Zell., *c*, mines the seed vessels, southern England, local; *N. speciosa* Frey, p, mines leaves, Lyndhurst, Hants.

PLUTELLIDAE: *Cerostoma sequella* (Clerck), *c*, England, rather local.

GRACILARIIDAE: *Lithocolletis geniculella* Rag. (*acernella* Zell.) *p* and *c*, mines on underside of leaves, feeds very high up (Ford), southern England, spreading since first recorded in 1925; *L. sylvella* (Haw.) (*acerifoliella* Zell.), *c*, mines on underside of leaves, southern England to York, common; *Gracilaria hemidactylella* (Fab.), *p*, in conically rolled leaves, England and southern Ireland, rare and local; *G. pyrenaeella* Chrét., *c*, in conically rolled leaves, Isle of Wight (Ford, 1933); *G. semifascia* Haw., *c*, in conically rolled leaves, England to York, very local.

OECOPHORIDAE: *Borkhausenia similella* (Hb.), *p*, under dead bark, also on *Pinus*, Staffs to Perth, southern Ireland, local.

GELECHIIDAE: *Telphusa scriptella* (Hb.), *c*, in folded leaves, England to Perth, local.

TORTRICIDAE: *Argyrotoxa forskaleana* (L.), *c*, England, common.

EUCOSMIDAE: *Pammene regiana* Zell., *p*, on seeds, England to York, Ireland, common (Ford); *P. trauniana* Schiff., *c*, on seeds, southern and eastern England, local.

NOTODONTIDAE: *Ptilophora plumigera* (Esp.), *p*, *c*, southern England, local; *Lophopteryx cucullina* (Hb.) (*cuculla* Esp.), *c*, south-east England.

GEOMETRIDAE: *Cosymbia annulata* (Schulz.), *c*, England, local; *Eupithecia inturbata* (Hb.), *c*, on flowers, England, local; *Hydrelia flammeolaria* (Rott.) (*Euchoeca luteata* Schiff.), *c*, in the north on alder, Britain to Caledonian Canal.

NOCTUIDAE: *Apatele* (*Acronycta*) *aceris* (1), *c*, *p*, *n* (O. W. Richards, MS.), also plum and horse chestnut, England to Lancs, common; *Tiliacea* (*Orthosia*) *aurago* (Fab.), beech and *c* when growing near beech, England to York, local.

DIPTERA

CECIDOMYIDAE: *Atrichosema aceris* Kieff., *c*, white larva (usually one) in elongate-fusiform purplish swelling of leaf petiole or occasionally basal part of mid-rib (Bagnall & Harrison, 1918); *Contarinia acerplicans* Kieff., *c*, *p*, folds spreading from edge of leaf on dorsal surface coloured red above, with white hairs below, with many white larvae (Bagnall & Harrison, 1921); *Dasyneura acercrispans* (Kieff.), *p*, leaves crumpled and rolled or folded, reddened, veins hypertrophied, numerous white larvae on upper surface (Bagnall & Harrison, 1921); *D. acercrispans* var. *rubella* (Kieff.), *c*, gall similar (Bagnall & Harrison, 1918); *D. tympani* (Kieff.), *c*, rounded pustule 4·0–8·0 mm. diam. on leaf (Hall, 1918; Bagnall & Harrison, 1921); *Massalongia aceris* Rubs., *p*, slight hollows, faintly discoloured, beneath leaves (Bagnall & Harrison, 1921).

HYMENOPTERA

TENTHREDINIDAE: *Heterarthrus* (*Phyllotoma*) *aceris* (Kalt.), *c*, *p*, larva in blister-like leaf mine, England, common; *Messa hortulana* (Klug), *c*, *p*, and a morphologically indistinguishable race on poplar, larvae in blister-like leaf-mine, England, rather local; *Pristophora subbifida* (Thoms.), *c*, *p*, widespread in southern England.

CALLIMOMIDAE: *Callimome* sp. bred from *campestre* seeds (E. W. Jones & B. M. Hobby).

ACARINA

PHYTOPTIDAE: *Phytoptus* (*Eriophyes*) *macrorrhynchus* Nal., *c*, *p*, red to brown pimples 1·0–2·0 mm. diam., on upper surface of leaf, often very numerous and cavity lined with white unicellular hairs, England and Ireland; *P. macrochelus* Nal., with six vars., *c*, *p*, galls of varying type on upper surface of leaves—the typical form is isolated glabrous pimples 2·0–4·0 mm. diam., cavity lined with brown pluricellular hairs, but the gall may also take the form of a patch of swollen hairs or of a pocket opening dorsally—England, widespread; *Phyllocoptes gymnaspis* Nal., *c*, *p*, gall consists of rows of normal or somewhat thickened hairs on underside of leaf, England, widespread; *P. acericola* Nal., *c*, *p*, gall a slight swelling on the upper surface of leaf at vein junction, depression beneath filled with somewhat swollen hairs, England, widespread; *P. aceris* Nal., *c*, British (Bagnall).

The following gentlemen kindly helped in preparing the foregoing list: Dr H. F. Barnes, Mr R. B. Benson, Mr W. E. China, Mr C. T. Gimingham, Mr F. Laing, Dr A. M. Massee, Dr G. D. Morison. Dr B. M. Hobby has also greatly helped in collecting records.

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INSECT VISITORS TO FLOWERS

THYSANOPTERA

Taeniothrips vulgatissimus (Hal.) and *T. atratus* (Hal.), *p*, (Morison MS.).

DIPTERA (Knuth, Poll. 2, unless otherwise stated)

Bibionidae: *Bibio hortulanus* (L.), *p*.

Syrphidae: *Syrphus ribesii* (L.); *Eristalis arbustorum* (L.), *p*; *E. tenax* (L.), *p*.

Empididae (E. W. Jones): *Empis tessellata* F., *c*; *E. pennaria* Fall., *c*; *Microphorus holosericeus* Mg., *c*; *Rhamphomyia longipes* Mg., *c*.

HYMENOPTERA

Tenthredinidae: *Tenthredo* spp., *c*, *p* (Benson, MS.).

Apidae (Knuth, unless otherwise stated): *Andrena haemorrhoa* (Fab.) (=*albicans* auct.), *p* (also Alfken); *A. tibialis* (Kby)., *p* (Alfken); *A. jacobi* Perk. (=*trimmerana* auct.), *c*, *p* (also Alfken); *A. nigroaenea* (Kby.), *c* (also Alfken); *A. bicolor* Fab. (=*gwynana* Kby.), *p*. Also the non-British *A. mitis* Pér. and *A. rufula* Pér., *p*. *A. bucephala* Steph., *p*; *A. cineraria* (L.), *p* (Alfken); *Anthophora aestivalis* Pér., *p* (non-British); *Melecta luctuosa* (Scop.), *p*; *Nomada marshamella* (Kby.) (=*alternata* Kby.), *p*; *N. ruficornis* (L.) (=*bifida* Thoms.), *p*; *N. panzeri* Lep. (=*ruficornis* auct.), *p*; *N. goodeniana* (Kby.) (=*succincta* auct.), *p*; *Osmia emarginata* Lep., *p* (non-British); *Bombus terrestris* (L.), *p* (also Kirby 1802); *B. lapidarius* (L.), *p* (also Sladen, 1912); *B. hortorum* (L.), *p* (also on isles of Coll and Rhum, Harrison, 1941); *B. ruderarius* (Müll.) (=*rajellus* Kby.), *p*; *Psithyrus barbutellus* (Kby.), *p*; *Apis mellifera* L., *c*, *p* (also Kirby and Alfken). According to Morison MS. *p* is a very important source of honey in north-east Scotland in May and June; some honeydew may also be taken.

COLEOPTERA (E. W. Jones)

Mordellidae: *Anaspis maculata* Fourc., *c*; *A. frontalis* L., *c*.

Nitidulidae: *Meligethes viridescens* F., *c*.

Cerambycidae: *Clytus arietis* L., *c*; *Grammoptera ruficornis* F., *c*.

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L.C. (Ed. 11) No. **369**

Acer pseudo-platanus L.

Sect. Spicata. A tree attaining a large size. Leaves, simple, isodiametric, dark green above, glaucous below, sometimes with reddish tinge; commonly 7–15 cm. (3–6 in.) across, glabrous except for some tomentum in axils of principal veins below; palmately five-lobed; lobed ovate, acute, extending about half-way to leaf base, coarsely serrate; base cordate. Petiole without latex.

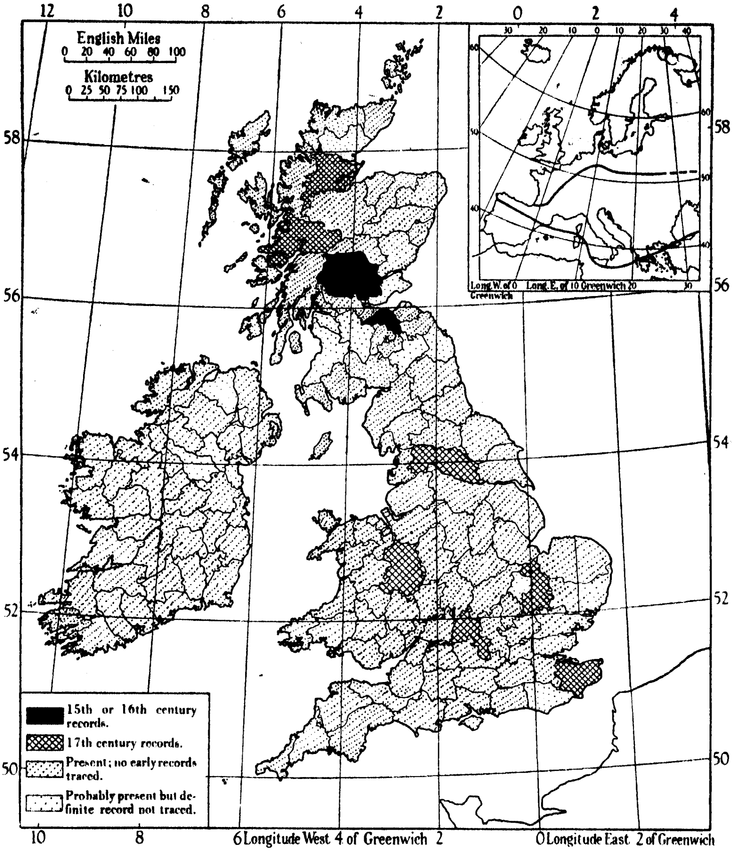

English Miles
0 20 40 60 80 100
Kilometres
0 25 50 75 100 150
15th or 16th century records.
17th century records.
Present; no early records traced.
Probably present but definite record not traced.
Long. W. of 0 Greenwich
Long. E. of 10 Greenwich 20 30
6 Longitude West 4 of Greenwich 2
0 Longitude East 2 of Greenwich
58
56
54
52
50

Fig. 1. *Acer pseudo-platanus* L; vice-comital distribution in the British Isles and (inset) probable limits of distribution as a native species in Europe.

Flowers in pendulous terminal racemes 7·5–20 cm. (3–8 in.) long, with 60–100 flowers. Fruit (of two samaras) glabrous with wings which are expanded towards apex, and either each straight and together forming an angle of 50–60°, or else incurved so that their apices are more or less parallel; length of each samara 3·5–5 cm. (1½–2 in.).

Petioles, peduncles and young twigs glabrous. Twigs stout, green when young, light brown in first year, bark later light or dark grey, thin, smooth and remaining so for many years: ultimately exfoliating in small thin rectangular oblong flakes. Lenticels small (up to 0·5 mm. across), round or shortly linear, buds large (to 12 × 8 mm.), ovoid, acute, brownish green to green, with several bud-scales; axillary buds projecting from twig (cf. *A. platanoides*, where they are erect). Leaf scars large, U-shaped, extending nearly halfway round twig, terminal bud scars conspicuous, occupying a wide zone.

Not very variable, though several forms of garden origin are in cultivation; cf. also VI (*i*). An introduced species long naturalized in Britain, tolerant as regards exposure and climatic factors generally, but exacting as regards soil, needing deep, freely drained, relatively fertile soils in order to thrive.

I. *Geographical and altitudinal distribution.* Spread by planting throughout the whole of Britain; although it has not been possible to collect records for every vice-county it is almost certainly present in all. Essentially a tree of the mountains of south and central Europe and Asia Minor, from the Pyrenees to Caucasus. The exact northern boundaries of region where indigenous greatly obscured by planting: it has been naturalized throughout the lowlands of northern Europe and has been claimed as locally indigenous in the Baltic region. Probable northern limits: Pyrenees, Auvergne, Vosges, Odenwald, Harz Mountains, Leipzig, Breslau, Kalisz (Poland) Lüblin, Cholm. Southern limits: north Spain, Sicily, Balkans, central Greece, Caucasus to lat. 35° N.

In Britain from sea-level at least to the uppermost limits of cultivation and habitation. Lees (1888) records 'well-grown trees' at 460 m. (1525 ft.) in Teesdale, and, judging from records in local floras, it is frequent to this altitude throughout the Pennines, Lake District, eastern Wales, Shropshire, etc. On the Clee hills (Shropshire) fruiting at nearly 480 m. (1600 ft.). Its potential upper limit is determined more by presence of suitable soil and regeneration conditions than by exposure or temperature. Thus in districts where the limit of enclosure is lower the upper limit of sycamore is also lower, e.g. Kerry, 270 m. (900 ft.) (Scully, 1916). Generally ascends higher than any other angiosperm tree except *Sorbus aucuparia* and *Betula* spp., though not as high as the conifers *Larix decidua* Mill. or *Picea abies* L. Upper limits, Harz Mountains 880 m., Bavarian Alps, 1510 m. as a tree, 1650 m. as scrub (Rubner, 1934); Hohen Tatra, 1500 m. Lower limit probably about that of *Fagus silvatica*; in the Bavarian Alps said to be about 575 m., but so confused by planting as to be scarcely traceable (Rubner, 1934); in the Danube Gorge said to be well defined at about 470 m., but even in south Europe often found at much lower levels where doubtfully indigenous (Fekete & Blattny, 1914). In Corsica ranges from 350 to 2000 m. (Briquet, 1913).

II. *Habitat.* In woods, plantations, hedges, and around houses, farms, etc. The following remarks on habitat, synecology, etc., in this country apply primarily to habitats where there is natural regeneration or stands of spontaneous origin.

Stands exposure to wind and to salt spray better than almost any other large deciduous tree, and hence it has been commonly planted around exposed farms in the hill country, e.g. of Pennines, Wales, western Ireland, etc., and on the sea coasts.

In general is said by Continental writers to require cool moist conditions. There is some diversity in statements regarding effect of aspect; it seems probable that (as stated by Hempel & Wilhelm, 1889) in drier regions and at low levels it prefers cool aspects (north and north-easterly), but in cooler wetter regions, as at high levels, it often prefers warmer aspects.

Continental writers all agree in saying that a deep, moist soil, freely drained and of relatively high base status ('strong') is required. It is characteristic of 'constantly moist loamy places on mountain slopes, gentle valley hollows, and especially narrow fresh valley floors of the higher montane and the alpine zones' (Gayer, 1898). It is commonly abundant on limestone, though Mathey (1924) states that where this is very pure (i.e.

weathering cleanly to give very shallow light soils), as in parts of the Jura, sycamore does poorly even when planted. Although liking moist places it will not tolerate waterlogging or inundation of roots.

In Britain, where naturalized, similar soil preferences are shown, although it will grow well and regenerate freely on almost any soil which is deep enough, sufficiently well drained, and not highly deficient in bases. It is very luxuriant on deep loamy sands and on light to medium loams such as those derived from the softer palaeozoic shales (cf. lists 12–16), the Old Red Sandstone and the felspathic Carboniferous sandstones.

It will thrive and regenerate on some of the highly siliceous Triassic and Tertiary sands, even when podsolized, provided the soils are deep, well drained and well aerated, as for example on deep colluvial soils (cp. list 11, p. 225). In East Anglia, though often regenerating profusely and growing rapidly when young (cf. V (*b*)), growth in general is relatively poor (A. S. Watt). It is especially luxuriant and profuse in regeneration on many of the heavier basic loams on Jurassic limestone (list 3), Carboniferous Limestone (list 5), and Clay-with-Flints over Chalk. Usually it does not regenerate on podsols nor on heavy clay where gleying comes close to the surface, and where planted in such soils is subject to root rot (W. R. Day). In Bishop Wood, Selby, it seems to reach its limit of occurrence where the maximum general height of the winter water table is about 30 cm. below the surface, the soil having fine faint mottling—perhaps indicative of occasional brief rises to a higher level—to about 18–20 cm. from the surface, and heavy gleying from 40 cm. downwards (cf. lists 6–8).

On shallow rendzinas on solid Chalk, regeneration may be profuse (list 1) though subsequent growth is poor; on rendzinas over Chalk rubble there may, on the other hand, be excellent growth. It occasionally spreads on to peat bogs (Cyb. Hib., 1898).

Those soils where sycamore naturalizes itself are almost invariably ones where humus decay is rapid and nitrification free; indeed, it is probably to some extent a nitrophilous species. It usually indicates a fertile soil, and there is a marked correlation between its occurrence and the 'quality' (i.e. height attained in a given time) of larch, spruce and pine, being more constant the better the quality.

III. *Communities.* In France, Germany, northern Switzerland, etc., it is commonly found in the region of beech and beech-silver fir forest, and usually occurs mixed singly with these species in suitable habitats. It is very often associated with ash, the habitat ranges of the two species largely overlapping, though ash is on the whole on somewhat heavier, wetter soils. In favourable localities, especially in moist hollows, small valley floors, etc., in the upper part of this zone there may be small communities of pure sycamore, or of sycamore mixed with ash (e.g. Swabian Alb (Hofmann, 1922); Haut Vosges (Issler, 1932) and elsewhere (Frank, 1927; Bergers, 1922)); but extensive pure stands never occur. Since it is very quick growing when young it is often abundant in young mixed crops, but the percentage present decreases as the crop ages and the sycamore is suppressed by the more tolerant beech (e.g. the Swabian Alb (Hofmann, 1922), Sihlwald, Zürich).

In Britain old trees of spontaneous origin are rarely, and unplanted mature stands possibly never, found, but in the pole stage pure stands of small extent are not infrequent. These naturally reflect the conditions under which regeneration takes place, and they will be more fully discussed in this connexion. Some examples will here be given of ground vegetation in spontaneous pole and coppice stands, and of communities where sycamore is regenerating, selected to give some indication of the range of habitat:

(i) *On chalk and limestone—herbaceous species and bryophytes*

	1	2	3	4	5
Rubus fruticosus	o.	o.-l.d.	.	c.d.	.
Hedera helix	.	v.a.-d.	.	c.d.	.
Mercurialis perennis	r.	l.o.	r.	.	l.a., a.*
Viola riviniana	.	f.	f.	r.	.
Fragaria vesca	.	f.	a.	.	.
Geum urbanum	.	o.	.	v.l.	.
Nepeta hederacea	r.	f.	.	.	.
Geranium robertianum	.	f.	.	o.	.
Sanicula europaea	.	o.	.	f.	.
Urtica dioica	r.	.	r.	.	.
Primula vulgaris	.	r.	.	.	o.*
Epipactis latifolia	.	.	f.	v.r.	.
Prunella vulgaris	.	l.a.	.	.	.
Circaea lutetiana	.	v.l.	.	.	.
Carex silvatica	.	f.	.	.	.
Arctium minus	.	o.	.	.	.
Arenaria trinervia	.	r.	.	.	.
Viola hirta	.	.	f.	.	.
Ajuga reptans	.	.	r.	.	.
Bromus ramosus	.	.	.	a.	.
Deschampsia caespitosa	.	.	.	v.l.	.
Anemone nemorosa	.	.	.	.	l.v.a., c.d.*
Scilla non-scripta	.	.	.	.	l.a., c.d.*
Conopodium denudatum	.	.	.	.	l.f.
Cardamine pratensis	.	.	.	.	r.*
Arum maculatum	.	.	.	.	f., o.*
Dryopteris filix-mas	.	o.	.	.	o.*
Eurhynchium praelongum	f.	a.	f.	v.a.	a.
Thuidium tamariscinum	v.l.	l.a.	o.	.	a.
Brachythecium rutabulum	v.a.	.	o.	l.	f.*
Mnium undulatum	f.	l.a.	.	.	f.
Eurhynchium striatum	v.a.	.	v.a.	.	.
Brachythecium purum	r.	.	v.a.	.	.
Fissidens bryoides	.	f.	.	l.	.
F. taxifolius	l.f.	.	.	.	.
Eurhynchium confertum	.	.	.	l.	.
E. piliferum	.	.	.	.	a.*
Catharinea undulata	.	.	.	.	a.
Plagiochila asplenioides	.	.	.	.	a.

(1) Inholm, Berks. Rendzina. 20–46 cm. (8–18 in.), medium loam and Chalk rubble over solid Chalk. 33-year-old plantations of *Pinus laricio*, *Larix decidua*, etc. Sycamore seedlings very abundant making 25–50 % cover; 3 years old.

(2) Bellowes Cross, Dorset. On Chalk. Mixed *Fraxinus*, *Pinus sylvestris*, *Larix decidua*, etc., *c.* 60 years old. Sycamore poles and seedlings abundant, seedlings going into shade where *Hedera* and *Eurhynchium praelongum* are only other species.

(3) Kiddington, Oxon. Rendzina on Oolite. 38 cm. (15 in.), heavy loam over weathered oolitic rubble. *p*H 7·0–7·6. 43-year-old *Larix decidua*, mixed with spontaneous sycamore of same age. Sycamore seedlings very abundant, making 20 % cover, 1–8 years old, and up to 20 cm. tall. Cover of other flowering plants, 1–2 %; *Mercurialis* and *Urtica* invading. Also present: *Fraxinus excelsior* seedlings rare. Rabbits abundant, sycamore poles badly barked.

(4) Wynward Park, co. Durham (Dr K. Blackburn). Boulder Clay over Magnesian Limestone; brown forest soil; red-brown clay. *p*H surface, 4·7; below 10 cm, 6·7. 115-year-old *Fagus sylvatica* with some sycamore. Saplings of sycamore, 2–30 cm. tall, frequent. Also present: saplings of *Fraxinus excelsior*, 30–60 cm. tall, o. *Crataegus monogyna*, f.; *Viburnum opulus*, o.; *Sorbus aucuparia*, r,; *Prunus spinosa* r.; *Rosa* sp., o.

(5) Yealand, Lancs. Brown forest soil or rendzina; very variable depth of brown loam over Carboniferous Limestone. Mixed *Fraxinus* and sycamore coppice and pole. Frequencies marked * refer to patches of pure sycamore. Also present: *Corylus avellana*, *Betula* sp., *Ulmus montana*, *Prunus avium*, *Sambucus nigra**, *Lonicera periclymenum*.

(ii) *On low-lying wet soils*

	6	7	8
Acer pseudo-platanus	c.d.	d.	d.
Betula pubescens	c.d.	r.	f.
Fraxinus excelsior	.	.	f.
Sambucus nigra	.	r.	.
Rubus fruticosus	a.	r.	a.
Lonicera periclymenum	f.	.	a.
Holcus mollis	d.	v.a.	a.-c.d.
Scilla non-scripta	v.a.	d.	v.a.-c.d.
Dryopteris filix-mas	a.	f.	a.
Digitalis purpurea	l.a.	.	.
Epilobium angustifolium	f.	.	.
Teucrium scorodonia	o.	.	.
Arenaria trinervia	.	v.l.	.
Allium ursinum	.	.	v.a.
Ajuga reptans	.	.	f.

In no. 8 only	
Viola riviniana	o.
Lysimachia nemorum	o.
Primula vulgaris	o.
Filipendula ulmaria	o.
Cirsium palustre	o.
Ranunculus ficaria	o.
R. repens	o.
Veronica montana	r.

Bryophytes (only listed for no. 7)	
Catharinea undulata	a.
Eurhynchium praelongum	a.
Lophocolea bidentata	a.
Plagiothecium denticulatum	f.
Dicranella heteromalla	f.
Plagiochila asplenioides	o.

(6)–(8) Bishop Wood, near Selby, Yorks. On warp clay. These three stands are within 20–30 yd. of each other, and form a sequence illustrating relation to ground water. All are on brown forest soils with tenacious, heavily gleyed basic blue clay at depth, and there is no water-table in late summer within 1·2–1·5 m. (4–5 ft.) of the surface. Nitrification free. *p*H measurements electrometric—glass electrode.

(6) Plateau site, poorly drained. Medium loam with fine mottling from 17 to 28 cm. (7–11 in.), distinct orange mottling from 28 to 41 cm. (11–16 in.), and heavily gleyed clay below. Winter water-table at about 30 cm. depth. At surface *p*H 4·15, very little exchangeable Ca; at depth *p*H 6·6 with very high exchangeable Ca content. Growth of sycamore poor, dominance shared with *Betula*.

(7) Mid-slope, freely drained. Soil a heavy loam, no mottling in upper 40 cm.; otherwise as in (6). Winter water-table below 45 cm. (18 in.). Optimum conditions for sycamore, which forms a pure stand and has much better height growth than in (6). Many of the differences from (6) in ground vegetation due to greater shade.

(8) Lower slope, wet, approximating to a meadow soil. Grey-brown clay; much ill-defined rusty mottling from 20 to 42 cm. (9–17 in.); heavily gleyed tenaceous clay below. *p*H at surface 4·5; at 60 cm. (24 in.) 6·6. Winter water-table at about 35 cm. (14 in.). At a slightly lower level on the slope with winter water-table at 25–30 cm. (10–12 in.), sycamore is absent, *Fraxinus* and *Alnus* being dominant.

(iii) *On sands*

(9) Bagley Wood, Berks, nr. Oxford. In a 30-year-old hardwood plantation (*Prunus serotina* Ehrhart) on Calcareous Grit. Brown forest soil. A deep basic heavy sand, freely drained. *p*H 7·0 (colorimetric). Nitrification free.

Mercurialis perennis	d., 20–100% cover	Arum maculatum	r.
Nepeta hederacea	f.	Conopodium denudatum	r.
Galium aparine	f.	Melandrium dioicum	r.
Urtica dioica	f.	Ranunculus ficaria	r.
Scilla non-scripta	o.-f.	Eurhynchium praelongum	v.a.
Adoxa moschatellina	o.	E. striatum	a.
Sambucus nigra	o.	E. piliferum	f.
Anemone nemorosa	r.-o.	Brachythecium rutabulum	f.
		Mnium undulatum	f.

Light conditions in this stand are marginal for sycamore regeneration, which is locally frequent.

(10) West Stow, Suffolk (Dr E. F. Warburg). Degraded brown forest soil. 71 cm. (28 in.) freely drained blown sand over Chalky Boulder Clay with imperfect drainage. Surface *p*H 5·2. 35-year-old mixed *Larix decidua* and hardwoods:

Sycamore seedlings	f.	Epilobium angustifolium	v.r.
Fraxinus excelsior seedlings	l.f.	Sambucus nigra seedlings	v.r.
Rumex acetosella	o.	Ranunculus repens	v.r.
Agrostis tenuis	o.	Brachythecium purum	r.-v.a.
Arctium minus	o.	B. rutabulum	o.-f.
Cynoglossum officinale	v.r.	Eurhynchium praelongum	f.
Holcus lanatus	v.r.	Hypnum cupressiforme	o.

(11) Bockhampton, Dorset. On Tertiary sand; probably formerly cultivated. Sycamore coppice; locally also *Castanea* coppice, and *Fagus* and sycamore standards. Frequencies marked * refer to pure sycamore coppice:

Hedera helix	c.d.-d.*	Rumex sanguineus var. viridis	l.f.
Scilla non-scripta	r.*-c.d.	Arum maculatum	o.*
Pteridium aquilinum	r.*	Dryopteris filix-mas	r.*
Rubus fruticosus	r.*-f.	Polystichum aculeatum	o.*
Melandrium dioicum	f.	Scolopendrium vulgare	o.*
Geranium robertianum	f.	Circaea lutetiana	l.r.*
Geum urbanum	f.		

(iv) *On palaeozoic shales and gravels. Herbaceous species and bryophytes*

	12	13	14	15	16	17
Pteridium aquilinum	.	.	d.	.	.	l.
Rubus fruticosus	o.	r.	f.	o.	o.	r.
R. idaeus	.	.	l.	.	.	f.
Lonicera periclymenum	o.	.	o.	.	.	.
Oxalis acetosella	f.	a.	f.	a.	l.d.	l.a.
Viola ?riviniana	f.	r.	o.	.	.	o.
Digitalis purpurea	f.	f.-a.	v.r.	.	o.	o.
Scilla non-scripta	.	l.f.	c.d.	.	l.a.-f.	.
Galium saxatile	.	.	o.	o.	l.a.	v.r.
Agrostis tenuis	.	.	.	o.	l.d.	l.
Lysimachia nemorum	o.	f.	v.r.	.	.	.
Mercurialis perennis	d.	v.l.a.	.	.	.	.
Circaea lutetiana	f.	v.l.o.	.	.	.	.
Primula vulgaris	l.o.	r.	.	.	.	.
Teucrium scorodonia	.	o.-f.	v.r.	.	.	.
Scrophularia nodosa	.	r.	.	.	.	r.
Deschampsia flexuosa	.	.	.	.	f.	r.
Holcus lanatus	.	.	.	.	l.a.	r.
Asperula odorata	l.f.	.	.	.	.	.
Fragaria vesca	l.f.	.	.	.	.	.
Geranium robertianum	o.	.	.	.	.	.
Anemone nemorosa	o.	.	.	.	.	.
Geum urbanum	o.	.	.	.	.	.
Hyperichum pulchrum	o.	.	.	.	.	.
Epilobium montanum	o.	.	.	.	.	r.
Luzula sylvatica	o.	.	.	.	.	.
Holcus mollis	.	.	f.	.	.	.
Melandrium dioicum	.	.	o.	.	.	.
Nepeta hederacea	.	.	o.	.	.	.
Deschampsia caespitosa	.	.	r.	.	.	.
Melampyrum pratense	.	.	r.	.	.	.
Agrostis canina	.	.	.	.	l.d.	.
Calluna vulgaris	.	.	.	.	o.	.
Vaccinium myrtillus	.	.	.	.	r.	.
Cardamine hirsuta	.	.	.	.	.	r.
Epilobium angustifolium	.	.	.	.	.	r.
Urtica dioica	.	.	.	.	.	r.
Dryopteris filix-mas	o.	o.	l.	.	r.	o.
D. dilatata	.	.	l.	f.	a.	f.-l.d.
Athyrium filix-foemina	.	.	.	.	r.	f.
Blechnum spicant	.	.	.	.	r.	.
Mnium hornum	.	f.	r.	.	f.-a.	f.
Catharinea undulata	l.a.	f.	r.	f.	.	.
Polytrichum formosum	.	.	.	o.	?a.	?r.
Plagiothecium undulatum	.	.	r.	.	a.	r.
Hypnum cupressiforme	.	.	.	o.	o.	f.
Eurhynchium praelongum	.	.	.	a.	.	f.
Dicranella heteromalla	.	f.	.	o.	.	.
Fissidens bryoides?	l.a.	.	.	.	.	.
Eurhynchium striatum	l.a.	.	.	.	.	.
Mnium undulatum	l.a.	.	.	.	.	.
Mn. cuspidatum	.	.	r.	.	.	.
Hylocomium loreum	.	.	r.	.	.	.
Hypnum schreberi	.	.	.	.	o.	.
Plagiothecium denticulatum	.	.	.	o.	.	.
Thuidium tamariscinum	.	.	.	.	.	r.
Pellia epiphylla	.	f.	r.	.	.	.
Plagiochila asplenioides	o.	.	.	.	.	.

(12) Vaynor, nr. Welshpool, Montgomery (Dr I. Manton). On Silurian (Wenlock) shale. Brown forest soil, 50–100 cm., light loam, freely drained, over shale. Nitrification free. 500 ft. alt. Mixed *Quercus*, *Fraxinus* and sycamore with a little *Ulmus glabra*, seedlings of last three frequent. Also present: *Corylus avellana*, f.; *Acer campestre*, *Ilex aquifolium*, o. This example is on a more basic soil than (13)–(17).

(13) The Heald, Windermere, Lancs. Silurian shale. Brown forest soil; deep stony light loam, slightly degraded at surface; *p*H 4·4–4·8; 0·03–0·07 % readily soluble CaO, and 0·02–0·04 % readily soluble K_2O (B. P.-Urquhart). High forest of *Quercus*, *Fraxinus*, *Castanea*, *Fagus*, sycamore, etc. *Mercurialis*, *Circaea* and *Arum* only near stream gullies with *p*H 5·1–5·7 and 0·1–0·3 % CaO. Phanerogam cover less than 10 %. Sycamore regeneration very profuse.

(14) Parc y Derw Goed, Llanderfel, Merioneth (N. Woodhead). Silurian shale. Brown forest soil; deep stony medium loam; freely drained. 800 ft. alt. Various crops; *Quercus* and mixed *Quercus*-conifer, with frequent sycamore saplings where ground is bare except for 5 % cover of bryophytes.

Also present: *Corylus avellana*, *Ulmus glabra*, *Sorbus aucuparia*, all rare.

(15) Smatcher, New Radnor. Silurian shale. Brown forest soil; 57·5 cm. (23 in.), light loam over shale; freely drained; nitrification free; altitude 367 m. (1225 ft.). 65-year-old *Castanea* and sycamore, with some *Larix decidua* and *Pinus sylvestris*. Sycamore seedlings abundant. Where pure conifers, a turf of *Agrostis tenuis*, *Galium saxatile*, *Oxalis*, etc., with few sycamore seedlings.

(16), (17) Benmore, Argyll (Dr V. M. Conway). Schistose gravels. Both soils described as podsols but no. 17 formerly cultivated, resembling a brown forest soil, and vegetation typical of the sites with sycamore regeneration in this region. Altitude 12–22 m.

(16) Boat House Wood. Podsol: A, 6 cm. grey-brown loamy fine sand. B, 1 cm. rusty bright ochre; C, 46 cm. bright brown loamy coarse sand merging to coarse gravel. 35-year-old *Larix leptolepis*. Sycamore planted with the larch had outgrown it. Sycamore regeneration, 1–2 years old, occasional. *Betula* and *Sorbus aucuparia* regeneration, very rare. Exceptional in having sycamore regeneration with *Calluna* and *Vaccinium*.

(17) Deer Park Wood. 0–19 cm. humic sandy loam; 19–61 cm. rich brown gravel. 30-year old *Picea excelsa*. Seedlings of sycamore and *Fraxinus* frequent, with abundant saplings near margins of stand. 10 % phanerogam cover.

IV. *Response to biotic factors*. See VI (*e*) and IX.

V. (*a*) *Gregariousness*. See III.

(*b*) *Performance*. Commonly attains a height of 18–24 m. (60–80 ft.), but Elwes & Henry (1906) record several trees over 30 m. (100 ft.) high (maximum 30 m. (105 ft.)). Buhler (1927) summarizes the information which is available regarding the growth of young plants. Growth rate relative to that of other species varies greatly with soil; thus on sand Scots pine and European larch grew faster, but on suitable soils such as limestones sycamore was amongst the fastest growing of all European species. Flury (1895) also found sycamore one of the fastest-growing species, being exceeded in the first few years only by *Alnus glutinosa*, *Betula* sp. and usually by *Acer platanoides*. Near Thetford, Suffolk, on a deep sand it has been recorded as growing even faster than Scots pine and European larch, producing annual shoots 1 m. long until a height of at least 5–6 m. is attained (R. G. Sanzen-Baker), while even Japanese larch is sometimes outgrown (cf. list 16).

Information from various sources regarding the rate of height and diameter growth is summarized in Fig. 2.

In a planted stand in Bagley Wood, Oxford, at 34 years of age the average diameter at 1·5 m. of the dominants was 15 cm. (6 in.); 40-year-old coppice stems were about 20 cm. (8 in.) diam. Diameter growth of isolated trees naturally much faster. Diameters of up to 2·7 m. (9 ft.) at about 1 m. above ground level are on record from the Continent, and there are a number of trees 1·8 m. (6 ft.) or more in diameter in this country (cf. X).

(*c*) *Effect of frost, drought, etc.* Much less sensitive to late frosts than most of the important deciduous species. Frost damage is sometimes seen on trees growing without shelter in exceptionally frosty places; the plants become very much branched and bushy, the annual shoots remaining short and thin, and the leaves stunted.

Frost damage of this kind is uncommon in the country as a whole, but is locally common in Yorkshire (e.g. near Selby), and is likely to be found elsewhere in frosty districts in eastern England such as Breckland. The frost of *c.* 16 May 1935 killed young shoots 12 cm. long at Thetford (R. G. Sanzen-Baker).

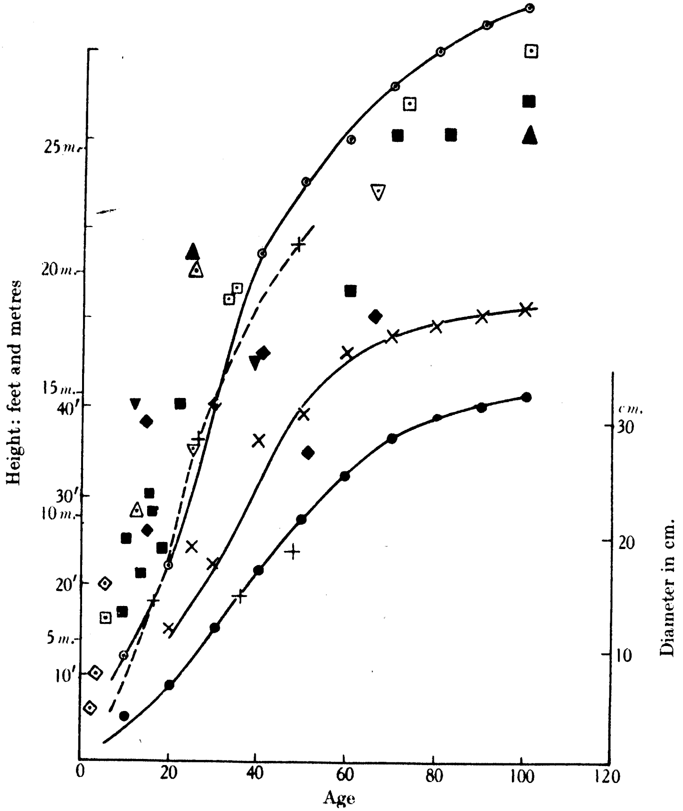


Fig. 2. Height and diameter of *Acer pseudo-platanus* and *A. platanoides*.

△ ▲ Scotland; ▽ ▼ Ireland, Wales and northern counties; ⊡ ■ Southern, midland and south-eastern counties; ◇ ◆ Foreign; Solid symbols, records from Loudon (1838); Hollow symbols, records from other sources, mainly unpublished.

-- + -- Bagley Wood, Oxford, height growth in closed stand on Plateau Gravel; the two lower crosses unconnected by a line and lying close to curve *B* are for diameter growth on the same site.

—⊙— *A. pseudo-platanus*, height growth on Muschelkalk; —●— *A. pseudo-platanus*, diameter growth on same site; — × — height growth of *A. platanoides* on same site Hartig (1851).

Frost rings in the wood caused by damage to the cambium have been recorded from the Continent by R. Hartig (1900), and from Edinburgh by J. Templeton (1923); they were, however, absent in material from Selby where twigs had been killed. Splitting of the trunk by frost is recorded from the Continent (Hempel & Wilhelm, 1889). Cankers which are probably caused by frost sometimes occur on small branches (W. R. Day). Some Continental writers say that the young seedlings are readily killed by frost (Jäger, 1841; Loffelholz-Colberg, 1845). Does not suffer from late frost in the Alps (Engler), but cannot be grown on account of frost in Lithuania and Esthonia (Rubner, 1934); it also suffers from frost in the German plains (The. Hartig, 1851). In the Faroes it suffers from both early and late frost (Börgesen, 1901–8).

Although relatively resistant to salt spray, foliage is sometimes scorched by it.

Stefanoff & Stoickoff (1932) class sycamore as one of the trees with very fluctuating water consumption during dry periods, and with considerable water deficit. In their experiments it usually transpired 12–30 % more water than was absorbed; this contrasts with *Fraxinus excelsior* and *F. oxycarpa* which transpired 60–90 % more than they absorbed but had a much lower water consumption, with *Fagus* having a smaller consumption and commonly no deficit, and with *Acer platanoides*, *Castanea* and *Quercus* spp. which also developed little or no deficit.

VI. *Morphology and vegetative biology.* (*a*), (*b*) *Root system.* On freely drained soils superficial skeletal roots are little developed, and in the mature tree the tap root is small. Typically has many heart roots descending at various angles from the stock making a relatively compact but deep root system. Engler (1903) gives the following account of roots of 1–3-year-old plants. Pronounced tap root absent; usually several strong lateral roots leave the root collar. The roots are rather richly branched: the absorbing roots of the 2nd year plant are of the 4th–5th order. Long roots (Triebwurzeln) specially well defined. Roots light coloured (paler than in other species except ash), remaining white in general colour even when growth has ceased and ultimately becoming pale yellow—therefore specially difficult to tell by inspection whether growing; frequently with brown patches and apex usually brown. Abundant root hairs present at all times—larger and denser than those of other tree species except ash; their distribution—whether to apex or not—some assistance in indicating activity of growth.

(*c*) *Mycorrhiza.* Endotrophic mycorrhiza of the 'Phycomycete' type are present, at least in superficial rootlets (Dr I. Levisohn; Renner, 1935). The same type of infection was present in seedlings from garden soil, in 'wild' seedlings and in older plants from several widely different soils. In first-year seedlings distribution of the fungus was rather sporadic, but in all older plants infection was very deep and widespread, the mycelium being of very large diameter. Active hyphae and digestion stages were present. Vesicles and arbuscules absent in May, but a few present in September (Dr I. Levisohn).

Shoot system. While the young seedling is very tolerant of shade older trees are very much less so. Once the lateral development of the crown has been severely restricted by competition with surrounding trees the stem rapidly dies of suppression, and trees with crowns so restricted show relatively slight powers of recovery when freed. Probably the relatively coarse nature of the branching, the brittleness of the twigs and a small number of dormant buds all contribute to this weakness. After the age when height growth is becoming slow sycamore is therefore very readily eliminated from mixed stands (cf. III), and this, as well as historical factors, may held to explain the rarity of old trees in woods. The trunk forks very readily, and repeated forking promotes the development of a very extensive spreading crown, such as is almost always shown by isolated trees or by trees in exposed positions or at high levels. Dimensions, leaf area, etc., see Table 2.

(*d*) *Perennation.* Mesophanerophyte with bud covering.

(*e*) *Vegetative reproduction.* Coppices very freely, to an age of 80–100 years (Loudon, 1838). Forms suckers only on poor light soils which are unsuited to it (The. Hartig, 1851); I have never observed these personally. There is no other method of vegetative reproduction. Jäger (1841), writing from experience of the Erbach forests (Odenwald, Germany), describes abundant sucker production up to a distance of 20–25 ft. from the stool following felling or coppicing; he also describes propagation by root cuttings.

(*f*) *Longevity*. There are authentic Continental records of isolated trees over 400 years of age, and the maximum age is probably about 600 years. In closed stand ages attained would doubtless be much less.

(*g, h*) *Production of seed*. Plants growing in open will start to bear fertile seed at from 20 to 30 years of age from seed; the 34-year-old stands in Bagley are still bearing very little seed (cf. stand 16, where regeneration was just appearing). Coppice shoots start to bear fertile seed at about 15 years. Isolated trees growing under good conditions certainly fruit freely annually, and most authors state that it fruits nearly every year. It is likely, however, that under less favourable conditions there is more irregularity; Hempel & Wilhelm (1889) and Hegi (Fl. 5) state that at high levels it fruits at 2–3 yearly intervals. At the higher levels in the Pennines the crop of seed is about half that at lower elevations, but is just as regular and as viable (Orde-Powlett). Engler (1905) found that seed from 1600 m. altitude was heavier and had a higher germination than that from 700–1100 m. altitude.

(*i*) *Ecotypes*. As with all trees which have been suitably studied seeds of sycamore from different climatic zones give plants which vary in rate of growth, time of leafing, etc. (Engler, 1905). Nothing is known as to the existence of such strains in Britain. Continental botanists have recognized several varieties and many forms of unknown status, some of which have leaves which are pubescent below, while var. *villosum* Pax, a southern form, has both leaves and fruits hairy. None of these forms have been recognized by British botanists.

(*j*) *Chromosomes*. $n = 26$ (Foster, 1933)

VII, VIII. *Phenology and reproductive biology*.

Growth of roots. 'Activity in the distal portion of the roots is very slow but continuous throughout the year' (Cockerham, 1930). Engler (1903) at Zürich also found very nearly continuous growth through the year, there being complete cessation only for a period of a few weeks in winter (for about 3 weeks ending 15 March in 1900), but with the usual periods of fast growth in spring—early summer and in autumn. Growth was more nearly continuous and more rapid in sycamore than in any other species studied, whether deciduous or conifer. Rates found for 2-year-old plants were:

73 cm. in 6-month period June–Nov. inclusive. Average per day for whole period 0·38 cm. Maximum growth for 10-day period, 1·1 cm. per day. Maximum growth for single 24 hr. period, 1·4 cm. Root growth ceased in winter when soil temperature around root apices fell to 1·6° C. (corresponding temperature for beech, 4·2° C.).

Cambial activity of stem. Swelling begins in late March (at Leeds), but cell division does not begin until 4–5 weeks later. Xylem only is formed at first; phloem formation begins in late June. Cambial activity ceases in mid-August (Cockerham, 1930). Belongs to 'the large ill-defined group...in which cambial activity begins on the twigs at various stages relative to the opening of the buds, and then spreads comparatively slowly down the tree, so that a considerable period may supervene before vessel differentiation may be recognized in the trunk' (Priestley, Scott & Malins, 1933).

Bleeds very freely, beginning in January earlier than almost any other British species except birch. Up to 3 % sugar in sap which has been used for extraction of sugar (cf. Loudon, 1838, p. 417).

Opening of buds. Buds of saplings growing beneath canopy, and of lower branches of trees in woods may begin to open by early or mid-March, but buds of upper crown do not open until about a month later. At Zürich at 680 m. alt. difference between time of first leafing of saplings beneath canopy and old trees is 13 days (mean of 12 years); old trees vary from 19 April to 22 May, mean 24 April; saplings from 1 April to 22 April, mean 11 April—later than in Britain. From 13 to 30 days, mean 22 days, elapses between first leafing and completion of leafing of old trees (Engler, 1911).

Height growth. Elongation of the shoot in mature trees is normally over and the resting buds formed by midsummer, but occasionally there is a limited amount of formation of lammas shoots; in 1943 growth of these had begun in Wilts on 3 July. Probably they are never formed by more than occasional trees. Elongation of seedling continues to mid- or late August (cf. Engler, 1905). Sycamore was exceptional amongst the trees studied by Engler (1905), in that when grown together the higher the altitude from which a strain was derived the later its date of leafing. Height growth also concluded earlier the higher the origin of the seed.

Time of flowering. Flowers usually open in about the first week of May in the southern counties, but varying from about 20 April to about 20 May according to season. Preston (1888) gives 21 April–22 May as the range for Wilts, 5 May being the average. The flowering period extends over about a month. Fruit increases rapidly in size, the oldest being 3 cm. long before the end of the flowering period.

Dispersal. Fruit ripe by early October; begins to fall in about last week of October (in September according to The. Hartig, 1851). In exposed places with high winds all fruit may be scattered within a few weeks, but normally falling is prolonged over the whole winter, and a few seeds may still be hanging on the trees as late as March, or occasionally May.

Dispersal by wind, usually over short distances only, though flights of 4 km. have been recorded (Hegi). Rate of fall about 0·9 m. per sec. (Dingler, 1889). Maximum distance of dispersal in 'tolerably strong breeze' from height of 15 m. (50 ft.) is 36–85 m. Collinge found seed in bird droppings (Ridley, 1930, pp. 72, 440).

Germination, viability. Seed will not germinate, even under favourable temperature conditions, before about mid-January. Under natural conditions the radicles emerge as soon after this as temperature conditions permit (e.g. often by early February), and cotyledons begin to appear above ground by early to mid-March. Germination of seed sown during this period is rapid and complete, even when it has been stored dry, but with further delay in sowing the period elapsing between sowing and germination rapidly becomes longer, and the percentage germination smaller, a proportion of the seed remaining dormant over the following winter. Thus seed sown on 17 February 1942 gave 92 % germination, beginning 13 days after sowing, while a sowing on 18 April 1942 gave 2 % germination, beginning after 40 days. 3–37 % of seed germinate in 20 days (Rafn, 1915).

Several authors (e.g. Baur, 1880; Loffelholz-Colberg, 1845, who recommends autumn sowing) state that the seed is slow and irregular in germination with a considerable proportion remaining dormant over the following winter, while Schlich (1910) and others give 50–55 % as being good germination. Rafn (1915) gives 65–82 % viability, mean 67 %, but with a higher proportion remaining dormant. It seems certain that such statements are due to sowing seed too late, and that, under natural conditions such dormancy and slow germination do not occur in this country. Several writers state that seed should be stored in moist sand. In my own tests, germination of over 90 % has resulted, even using seed stored dry in an ordinary room; Engler (1905) also found 80–96 %

germination. The seed is, however, sensitive to conditions of storage; and some of the lots which I have stored in the open throughout the winter have decayed.

Flowers. The elongate racemes each have up to a hundred flowers, of which 60 % or more, including all those on the distal part of the raceme, are male. The earliest flowers to open are male. The proportion of male to hermaphrodite flowers varies greatly from tree to tree. It is possible that entirely male trees occur, but it is difficult to establish this, and if they exist they must be rare; Hegi says that they are apparently absent. Trees with few hermaphrodite flowers are not uncommon, however; in roadside trees in the Cotswolds near Oxford fruit could not be seen on an average of 7–8 %; 14 % was the highest proportion for one population, and 33 % of the trees bore abundant fruit (1942). Age seems to have some effect on the proportion of male flowers, this being higher in younger trees.

The flowers are scented and produce nectar. They are energetically visited by honey bees and solitary bees (*Andrena* and *Halictus* spp.), *Bombus* spp. and to a less extent by many other insects, especially large Diptera (e.g. *Bibio* sp.).

Cleistogamy and vivipary do not occur. Reproduction probably amphimictic. No hybrids have been recorded.

Amount of fruit. Up to about 30 fruit per raceme are produced. For estimates of the quantities of fruit on trees, and also of amounts of foliage, etc., see table.

Table 1. *Average weights of samaras, embryos, etc.*

Without wings	0·0737–0·0892 g. 0·083–0·091 g.	Mean 0·0813 g. Rafn (1915) Schlich (1910) and others
Without wings: Switzerland, varying according to altitude	0·053–0·116 g.	Engler (1905)
Oxford, entire samaras: Sample *a*	0·200 g.	
Sample *b*	0·160 g.	
Do. without wings, sample *a*	0·171 g.	
Do. embryo only, sample *b*	0·135 g.	

Table 2. *Amounts of foliage and fruit on* Acer pseudo-platanus *and* A. campestre

Weights, areas and frequency distributions of leaves of various size classes determined on random samples from different parts of crown. Tree 1, all leaves and fruit weighed. Tree 2, foliage and fruit on samples of branches weighed. Tree 3, foliage on sample of branches weighed; complete count of number of bunches of fruit with determination of mean number of fruit per bunch in a 10 % sample. Trees 2 and 3, total lengths of leafy branch in crown measured. (1) In closed stand, Bagley Wood, Oxford. (2) Isolated tree in garden, Oxford. (3) Coppice stem in closed stand, Bagley Wood.

	A. pseudo-platanus		*A. campestre*
	1	2	3
Age	48	20	41
Height	19·1 m. (58 ft.)	10 m. (30 ft.)	14·4 m. (48 ft.)
Diameter at 4½ ft.	19·0 cm. (7·5 in.)	12·5, 13 cm. (two stems)	14·8 cm. (5·8 in.)
Length of crown	6 m. (20 ft.)	4·6 m. (15 ft.)	8·2 m. (27 ft.)
Diameter of crown	3·9 m. (13 ft.)	6·1 m. (20 ft.)	1·83 m. (6 ft.)
Total leaf area (one face only)	52·7 m.^{2}	*c.* 45 m.^{2}	11·6 m.^{2}
Total dry weight of foliage	3·3 kg.	5·33 kg.	0·908 kg.
Number of leaves	8970	4400	12,000
Mean area of one leaf	58·83 cm.^{2}	99·14 cm.^{2}	From 8·46 (upper) to 11·30 cm.^{2} (lower leaves)
Mean dry wt. of one leaf	368·4 mg.	1225 mg.	From 88 mg. (upper) to 67 mg. (middle leaves)
No. of seeds	870	9350 in 360 inflorescences	3096 in 834 inflorescences*
Total weight of fruit	175 g.	1870 g.	—

* Spread over 6·7 m. (22 ft.) of crown, but 89 % in upper 1·8 m. (6 ft.).

The seed has a high percentage viability apart from the undersized and obviously empty ones which are always present at the apex of the raceme and which form from 10 to 30 % of the crop. Insect attack in many samples is completely absent, and rarely affects as much as 10 % of the seed. There are frequently a few seeds (*c.* 2 %, but 8 % recorded in one sample) in which the embryo is soft and waterlogged.

Place of germination—biology of seedling. Germination is epigeal. The cotyledons are stout, 4–5 × 0·6–1·0 cm., glabrous, smooth, strap-shaped, narrowed at base, apex obtuse, with three obscure parallel veins; hypocotyl reddish at apex (Fig. 3). Buhler's (1927) experiments show that sycamore, in contrast to most species tried, germinated profusely in the dense shade of the forest, their percentage survival and length of survival actually exceeding that of beech, and being very much greater than that of ash. Sycamore is accordingly often one of the first phanerogams to appear on the bare floor of young conifer plantations, persisting with about the same light intensity as *Mercurialis*, *Urtica* and other species tolerant of deep shade. Sometimes indeed it actually precedes these species, probably because of its more rapid spread by seed (cf. list 3). It has been noted that ash and sycamore are often associated: regeneration of the two species is often mixed, when the greater vigour and persistence of sycamore in deep shade is very noticeable, the prevailing light intensity often determining whether an area seeds up with ash or sycamore (cf. Pearsall, 1922; Watt, 1925; see also list 4) (soil variation may also affect this distinction—cf. below). It is perhaps slightly less tolerant than regeneration of *Sambucus* with which it is also often associated. In the open where there is no competition the sycamore seedling shows no sign of suffering from lack of shelter. It is, however, intolerant of competition; Elwes & Henry (1906–13) and Hempel & Wilhelm (1889) note that in the early stages it is readily suppressed by grass, and it is a common experience that when planted in turf, e.g. in afforesting pasture land, it makes little growth for some years; in such conditions also it responds well to weeding (W. R. Day, R. G. Sanzen-Baker). It is rare to find regeneration in the open under natural conditions. When seedlings are found in grassland it is usually in thin closely grazed turf, often where seed which has been carried into the soil, e.g. by worms, germinates in the little patches of bare soil. Naturally under these conditions continued grazing prevents any establishment of seedlings.

On the other hand, it regenerates profusely in the moderately deep shade of woodlands where there is at most a thin and discontinuous carpet of herbaceous species and little litter, with plenty of mineral soil exposed. Beech and sycamore canopy casts too dense a shade for prolonged survival, but slow growth is made beneath oak, larch, ash, etc., growth being considerably improved if the stands are thin and irregular; in such stands it often forms an understorey. Watt (1925) describes it as forming an understorey 40 ft. high beneath an oak-ash-birch canopy. It often seeds up gaps in conifer plantations where practically bare ground has been offered for colonization, or bare ground beneath conifers or beech where there is sidelight, e.g. near the margins of plantations. The dense thickets of saplings which are formed under such conditions are very often even-aged. Seedlings and small saplings often form an important constituent of the field layer communities of woods. In Wychwood (Oxon.) it has been noted as entering pure European larch plantations after a period varying from about 35 years on the heavier and more basic soils to 50 or more on drier and degraded gravels. In a deciduous plantation in Bagley Wood (cf. list 9), where light conditions are marginal for survival of sycamore,

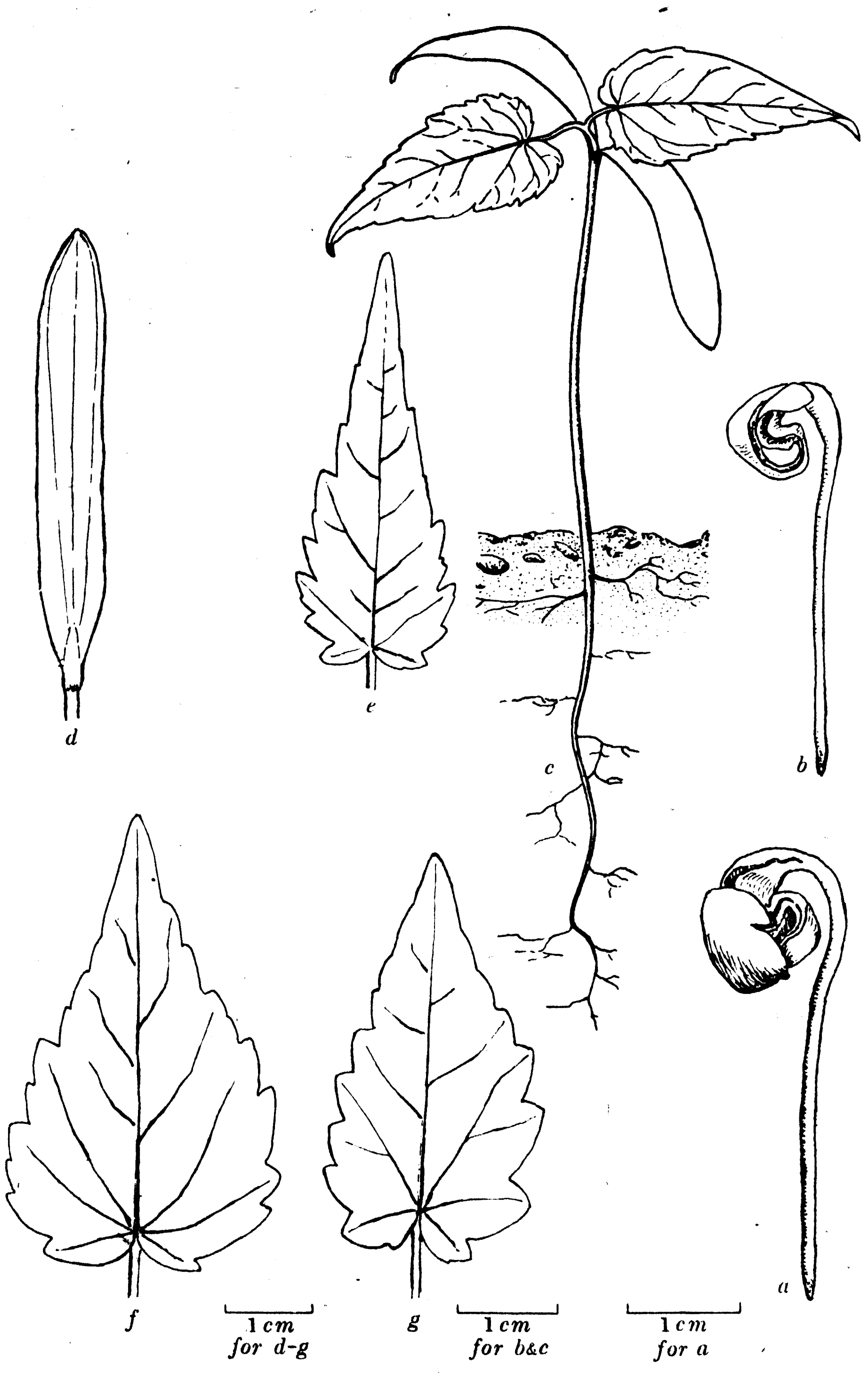


Fig. 3. *Acer pseudo-platanus* L.

(a), (b) Young seedling; in (a) the cotyledons are still within the testa; the fruit wall and wing have fallen away. (c) Seedling at later stage. (d) Cotyledon. (e)–(g) First foliage leaves from different plants.

the diurnal range of light intensity is from 0·0075 to 0·03 of full outside light where there is no regeneration, while a light intensity of 0·01–0·04 permits establishment. (Means of four series of readings on different days in late summer—maximum canopy density.) Wiesner (1907, cf. p. 141) found the minimum 'Lichtgenuss' in Steiermark to be $1/42 = 0{\cdot}024$.

Soil factors often also control the incidence of regeneration. Sometimes these doubtless operate directly, sometimes indirectly through determining the amount and nature of other vegetation; thus in some old hard-wood crops in Bagley Wood, there is a narrow region, where there is a relatively light colluvial surface soil of Plateau Gravel material over Kimmeridge Clay in which sycamore regenerates freely. At higher levels than this, on deep plateau gravel, regeneration will take place in the absence of *Pteridium*, but is normally prevented by its presence, sycamore also fails to regenerate on the heavier wetter clay soils lower down the slope, where, however, *Fraxinus* regenerates freely. Failure to regenerate on sticky clays even where basic can be observed repeatedly, e.g. on Oxford Clay and clays of the Lias. (See also lists 6–8, p. 224, for effect of water-table and differentiation by soil between sycamore and ash.) Failure to regenerate can also often be observed on degraded base-deficient soils. It will regenerate freely in conifer litter on suitable soils.

Seedlings are frequently associated with almost all of the common mesophytic shade species of basic soils. Their distribution often coincides with that of *Mercurialis*, e.g. with increasing wetness of soil the two often cease to occur at the same point. On non-basic soils *Rubus idaeus*, *Dryopteris dilatata*, *D. filix-mas*, *Adoxa moschatellina* and *Melandrium dioicum* are frequent and characteristic associates (see lists 11–17). Probably the non-basic soils where sycamore regenerates are almost always ones which, in the open, would be colonized by *Pteridium* rather than by *Calluna* or *Vaccinium*.

In addition to *Mercurialis* and *Urtica*, mentioned above, sycamore regeneration is very often accompanied by seedlings of *Sambucus nigra* and by the mosses *Eurhynchium praelongum* (very constant on a wide range of soils) and *Brachythecium rutabulum*. It is probable that the seedlings are somewhat nitrophilous; in Bagley Wood sycamore regeneration is associated with presence or production of nitrates in the soil except on rendzinas. W. H. Pearsall's records also show constant association of regeneration with presence of nitrates; he records sycamore regeneration from a *p*H of 4·11 upwards in the north of England.

Proximity of trees to give seed is also essential for profuse regeneration; circles of regeneration are often found around the parent trees.

IX. *Parasites; diseases.* See introductory notes on *Acer*. Mice avidly seek the seed and store it in caches (cf. *A. campestre*, VIII). Hegi (Fl. **5**) states that squirrels, crossbills and finches eat it. Rabbits browse on the foliage and twigs of seedlings, though to a much less extent than on some trees; Watt (1925) describes them as immune to rabbit attack. In woods where rabbits are abundant it is not uncommon to find abundant seedlings and small saplings even though poles are being killed by barking (cf. stand 3). The latter damage is done during winter, and is most severe with poles of *c.* 3–4 in. diameter (7·5–10 cm.), but in severe weather much larger trees are sometimes attacked; not until the bark is rough is the tree immune (Orde-Powlett). Grey squirrels sometimes also do severe damage by barking, sycamore being specially selected for attack. In a locality where poles of ash, beech and *Aesculus* were also available I have seen isolated sycamore poles *c.* 3 in. diameter completely stripped of bark from base to apex. Barbey (1942) in Switzerland records barking of poles below ground level, with fatal results, by water vole.

Deer browse the foliage (Hegi (Fl. 5) states that it is valued for fodder), but several writers, both Continental and British, state that it is not barked by deer; Evelyn (1662) says that it is specially commended for parks 'as least apt to spoil of deer'. Urquhart, however, records stripping of bark by deer.

Slugs and snails enjoy the cotyledons and are apparently responsible for many casualties among the seedlings (Jäger, 1841; Urquhart).

Lathraea squamaria has been recorded on the roots (Airy Shaw, 1944, A. E. Robins).

X. *History.* Frequent in some Continental interglacial deposits, e.g. near Paris and in Switzerland (Hegi, Fl. 5) but unrecorded fossil from Britain. The name 'sycamore' is a transliteration of the Greek *συκόμορος* = *Ficus sycamorus*, and this is almost identical with the Hebrew name for the tree, šiqmā. The word first appears in English in the fourteenth century, when it is used referring to the tree of the Scriptures, e.g. by Wycliffe, 1382. Chaucer speaks of a table of sycamore (*House of Fame*, line 1278), but it appears to have been a rare word until the early sixteenth century; the *Oxford Dictionary* cites no fifteenth-century examples of its use. Shakespeare speaks of the 'shade of the sycamore' in *Love's Labour's Lost* and of a 'grove of sycamore' in *Romeo and Juliet.* It is practically impossible to draw any deductions respecting the presence of sycamore in Britain from these references. *Ficus sycamorus* was apparently unknown to English people until the seventeenth century; the *Oxford Dictionary* gives 1615 as the earliest use of sycamore specifically for that tree. Thus these early writers may have used the name without connecting it with any familiar tree; if they did associate it with any tree known to them it is likely that it was with *Acer pseudo-platanus.* Both sycamore and maple are unmistakably represented in carving on the shrine of St Frideswide in Christ Church, Oxford (A.D. 1282). In French 'sichamore' appears in the thirteenth century (Littré, *Dictionnaire*).

Loudon states that the first record for Britain is by W. Turner in 1551; Druce also cites this record. This is an error, however. In Part II of Turner's *New Herball* (1562, not 1551) under 'Plane' is the following passage which clearly refers to *Acer pseudo-platanus*:

> 'Some take Ahorn to be *Platanus*...seemeth to me a kind of *Acer*. This grows in ye hyghest mountaines that are from [*sic*] thyng moyste, amongst the ashe trees. This tree is frequent in Germany.'

It may be deduced from this that Turner knew the sycamore on the Continent, but that he had not seen it in England, and that he was probably not familiar with the name sycamore as applied to it. Turner was a north-country man and knew Yorkshire and Northumberland, where sycamore is now a very common tree; he also shows familiarity with Cambridgeshire, Essex, Kent and Somerset.

The following are the references from other early botanical works:

H. Lyte (1578) in the *Nievve Herball* (p. 574): 'There is found in the Alpes in Almaigne and some places of Brabant a certayne tree much lyke to the plane...' 'is founde upon high mountaines in some places of Douchland and Brabant and amongst the feeldes, but very seldome, and there is here and there a tree of it planted in Englande.' 'Called in English Plane, French Plane, High Dutch Ahorne...is a kind of maple.' This is the first record of its presence in England in botanical literature; the passage does not occur in Dodonaeus, and is apparently an original statement by Lyte.

J. Gerard (1597), in *The Herball*, p. 1300: 'The Great Maple is a stranger in England only it groweth in the walkes and places of pleasure of noblemen where it especially is planted for the shadow sake, and under the name of sycomore tree. Acer major, The Great Maple, not rightly called the Sycomore. Ahorne, Waldeschern.'

J. Parkinson in the *Paradisi* (1629): '...cherished...only in Orchards or elsewhere for shade and walkes, both here in England and some other countries also...and hath no other use with us that I know.'

J. Evelyn in *Silva* (1662): 'The sycamore, or Wild Fig-tree, falsely so-called, is our Acer majus...much more in reputation for its shade than it deserves; for the Honey-dew leaves...contaminate and mar our walkes.' '...excellent for trenchers, cart and plow-timber...the more tolerable for distant walks. ...Some commend them to thicken copses, especially in parks, as least apt to spoil of deer, and that it is good fire wood.'

Ray in *Synopsis* (1690): '*Acer majus.* In coemitariis et circa nobilium aedes; nullibi, quod sciam, in Anglia sponte oritur.'

Almost every later botanical writer for over a century states that sycamore grows in hedges and about houses.

In Irish legislation of 1723 (Tenth year of Geo. I, Cap. IX, Sect. VIII) it is specified that butter casks 'shall be made of good seasoned Oak, Ash or Sicamore, whereof no part shall be boggy timber...'; only oak and ash were permitted by similar legislation in 1715. In an Act of 1768 it was included in a list of trees the felling of which was restricted (M. S. Anderson).

The general picture from these records seems clear; in the mid-sixteenth century sycamore, if present in the country, was sufficiently rare for Turner not to be aware of it, but it was present though still rare by 1578. Its cultivation was increasing rapidly through the late sixteenth and early seventeenth centuries, however, so that by 1662 it was sufficiently common to be banished by Evelyn to 'distant walks' and to be used for carts and ploughs.

There is, however, evidence of the cultivation of sycamore in Scotland in the fifteenth century. At Kippenross House, Dunblane, there was formerly a sycamore of very great size; a plate attached to this tree and dated 10 June 1842, gave as its dimensions in 1841, girth of smallest part of trunk, 19 ft. 6 in.; height, 100 ft.; extreme width of branches, 114 ft., age 440 years. It is not possible at present to ascertain the evidence on which this age was assigned (Lt.-Col. J. A. Stirling); if correct, however, it indicates planting in 1401.

According to Hunter (1883) there were at Castle Methven, Perth, some very old sycamores existing as remnants of avenues which were laid out around the old castle. This castle was built in 1487 and destroyed in 1502, and the site then abandoned. The trees were therefore almost certainly planted between these two dates. Loudon (1838) mentions a tree at Calder House alleged to date from about 1520, and Elwes & Henry (1906–13) record some at Newbattle Abbey near Edinburgh 'known to have been planted before the Reformation'.

It thus seems possible that sycamore was grown in Scotland at an earlier date than in England. There is some further indirect evidence of this. *A. pseudo-platanus* is commonly called 'plane' in Scotland, and as early as 1629 the English writer T. Johnson calls it 'Platanus Scoticus'. Although in botanical circles 'Bergahorn' is always said to be the German name, the ordinary German calls it 'Platane'. Early Continental writers also indicate confusion with plane, but do not mentioned the name 'sycamore'; the reference of John Bauhin 'Acer majus, multis falso Platanus' is typical. The French use the name 'sycomore' to some extent in place of the more correct 'érable de montagne', but otherwise it seems to be essentially an English appellation. It seems very probable that the tree was imported, with its common name of plane, direct from the Continent to Scotland. It is also curious that all the records of early plantings and exceptionally large trees given by Loudon and Elwes & Henry should come from Scotland; this, however, may be partly because no one has troubled to collect English records. Thus a sycamore at Loton Park, Salop, which is 93 ft. tall and 23 ft. girth, and said to be over 300 years old (Orde-Powlett, 1926), is considerably larger than any of those recorded from Scotland, and is probably the largest in Britain.

The following are some of the earlier records (prior to 1750) for England which I have found:

Shropshire, *c.* 1620 (tree at Loton Hall). Kent, 1629 (T. Johnson, '*Iter.*'). Cambs, 1660 (Ray). Oxford, 1677 (Plot, *Natural History of Oxfordshire*, pp. 172, 174; cultivated in Magdalen Grove and New College garden). Yorks, 1690 (planting at Bolton Abbey, Orde-Powlett). Northants, 1712 (Druce, 1930). Norfolk, *c.* 1740 (planting at Holkham Hall by Walpole).

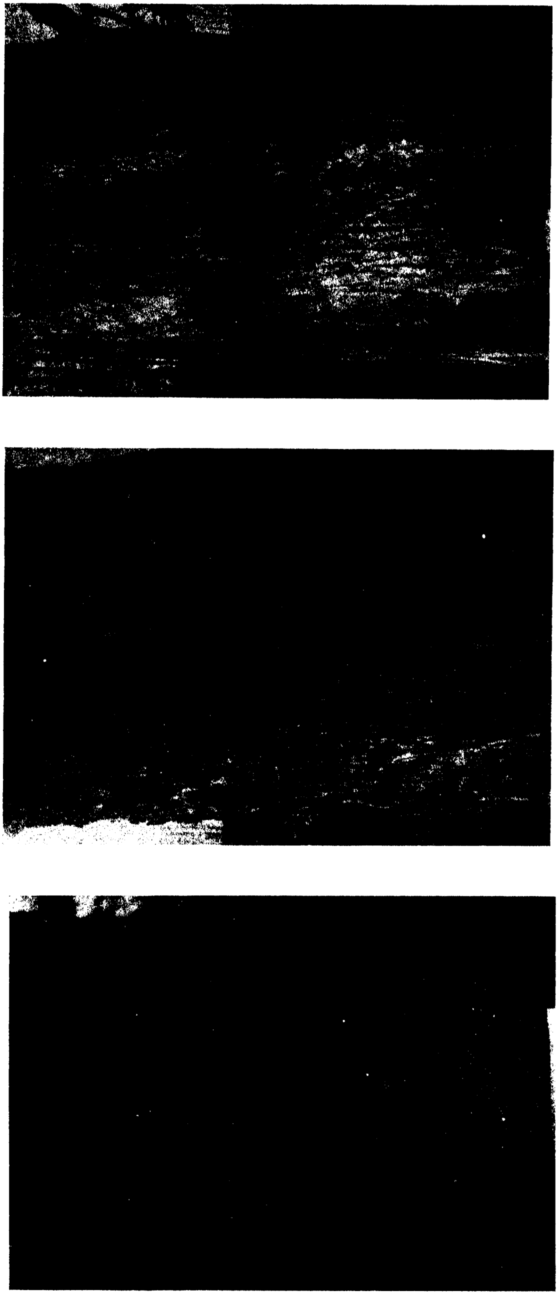
It seems probable that sycamore was little planted except as an ornamental tree in avenues, parks, etc., until the closing years of the eighteenth century, when it began to be more widely used in shelter belts, plantations, etc. There certainly was a very big extension of its use about this time when innumerable new parks were being made, and in many places where it is now naturalized there is evidence of planting at this period. Out of twenty-four Dorset woods in which sycamore is present, twenty were not shown on the first Ordnance Survey in 1811, while three of the remaining four are in parks where planting at a slightly earlier date is probable. The first flora to give its habitat as 'woods' is that of Bedford by Abbott (1798), though Lightfoot (1778) in the *Flora Scotica* says that it grows 'near houses and in Gentlemen's plantations'. Samuel Hayes (1794) comments on 'a vigorous growth of young sycamore from the keys of different ages and sizes up to twenty feet high or more, amidst old Scots Fir' as being a 'circumstance which I have not noted elsewhere'. This was at Luttrelstown, Co. Dublin. Hayes seems to have known the estates of south-eastern Ireland well, and to have been a careful and reliable observer. This is the first record of natural regeneration which I have found. It seems probable that had it been much planted in woods before the nineteenth-century, old trees of spontaneous origin, and perhaps old spontaneous stands would be far commoner than they are.

Acer platanoides L.

Acer platanoides, the Norway maple, was introduced in 1683 (Loudon, 1838) and has been far less extensively planted than sycamore but is occasionally found in woods where it frequently regenerates freely. Continental range wider than that of sycamore; northern boundary central France, south Norway and Sweden, Lake Ladoga, Urals; southern boundary north Spain, north Italy, Balkans, Asia Minor and north Persia. Ascends to 1000 m. in Switzerland.

Readily distinguished from sycamore by the leaves with acuminate, coarsely sinuate dentate lobes; flowers in short erect cymes; fruit large, wings widely divergent as in *A. campestre.*

Closely resembles sycamore in most features of its biology, e.g. soil preferences and tolerances, rapid growth, tolerance of shade and competition. It flowers about three weeks earlier than sycamore, just before the leaf buds open, and the flowers are energetically visited by *Bombus* spp. and *Andrena* spp., etc. It begins to fruit at a rather younger age than sycamore, and never reaches such a large size (cf. Fig. 2, p. 227). The seeds usually remain dormant throughout the first season after falling. Regeneration takes place under similar conditions to that of sycamore, and seedlings of the two species often occur together. Regeneration is sometimes profuse, and it would only need more extensive planting to become as fully naturalized as sycamore.


(a) (b) (c)

Phot. 1. *Acer campestre*. Three stages in bark of trunk: (*a*) about twenty years old; (*b*) old tree before exfoliation; (*c*) old tree after exfoliation. (*a*) × ½; (*b*) and (*c*) × ¼.

L.C. (Ed. 11) No. **370**

Acer campestre L.

Sect. CAMPESTRIA. A small tree. Leaves simple, isodiametric, usually about 5 cm. long by 6·5 cm. wide (2 × 2·5 in.), but up to 10 × 15 cm., palmately five-lobed, the basal lobes small, sometimes obsolescent or absent, lobes obtuse or acute, bluntly pointed, the three main lobes usually with a blunt tooth on each side, but sometimes entire, sinuses acute, base truncate to cordate; short hairs on veins above, below with long hairs on veins and blade thinly pubescent. Petiole as long as blade, more or less pubescent, with milky latex. Young twigs smooth, light brown, more or less pubescent, sometimes developing corky wings when 4–5 years old, lenticels inconspicuous. Buds brown with several scales, axillary buds erect. Bark light grey, when 20–30 years old rather smooth and hard but with shallow anastomosing regular fissures; ultimately when 80–100 years old exfoliating in small conchoidal flakes, leaving a rather smooth but cracked surface. Fruit a samara, 2–3·8 cm. (0·8–1·5 in.) long; wings of the two samaras usually at an angle of about 180° to each other; wing usually glabrous and body of fruit pubescent (var.

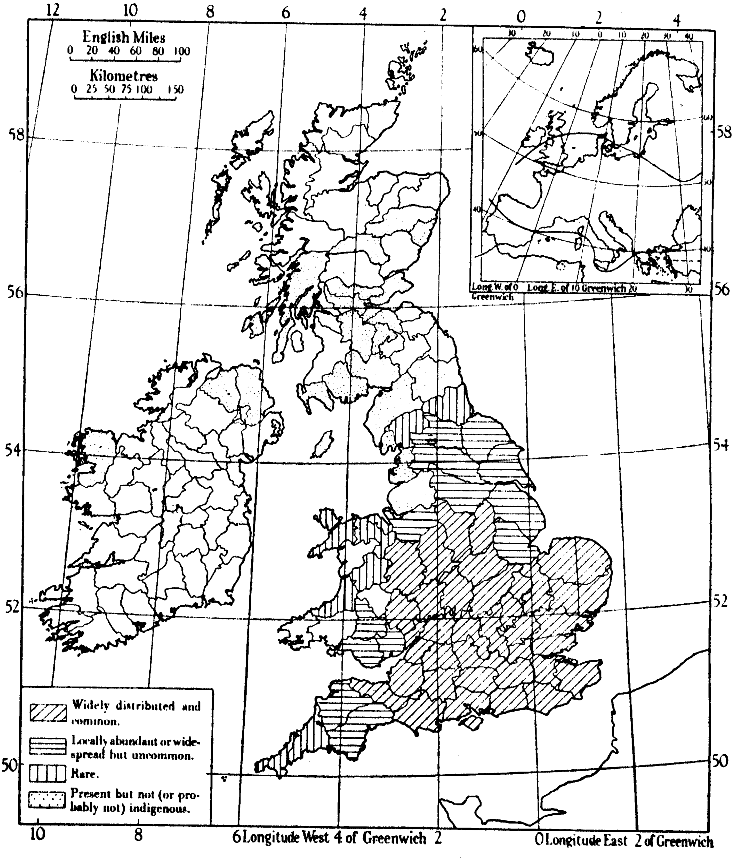

English Miles
0 20 40 60 80 100
Kilometres
0 25 50 75 100 150
12
10
8
6
4
2
0
2
4
58
56
54
52
50
▨ Widely distributed and common.
▤ Locally abundant or widespread but uncommon.
▥ Rare.
⬚ Present but not (or probably not) indigenous.
10
8
6 Longitude West 4 of Greenwich 2
0 Longitude East 2 of Greenwich
Long. W. of 0 Greenwich
Long. E. of 10 Greenwich 20 30

Fig. 1. *Acer campestre* L. Vice-comital distribution in the British Isles and (inset) distribution in Europe and North Africa.

hebecarpum DC.) but sometimes villous with long hairs, or glabrous (var. *leiocarpum* Opiz).

A southern species in Britain, tolerant of shade, and very characteristic of woodland on basic soils, especially when heavy. Coppices freely.

There is considerable variation in leaf form—e.g. in depth of lobing, angle of sinus, shape of lobes, and in the direction of the basal lobes (their veins usually form an angle of about 90° with the midrib), and also in the form and hairiness of the fruit. Usually the proximal margin of the fruit wing is nearly straight, the two together forming an angle of 180°, and the wing is little expanded towards the apex. Forms, however, occur in which the margin is reflexed, sometimes strongly, and in which it is inflexed. The apical leaves of a stem are more deeply and narrowly lobed than the lower leaves, and the leaves of young coppice shoots still more deeply incised. The var. *leiocarpum* Opiz was elevated by Pax to the rank of an 'apparently very distinct subspecies' (Hegi, Fl. **5**) and both 'subspecies' *hebecarpum* and *leiocarpum* divided into several varieties, mostly defined by single characters. Many of these variants occur in England and are certainly genotypical, as comparison of neighbouring trees growing under identical conditions shows, but it is very doubtful whether distinct taxonomic units can be recognized. There is no correlation between hairiness of fruit and any other character of fruit or leaf, except that the petioles and stems of glabrous-fruited plants are often (but not constantly) less hairy.

I. (*a*) *Geographical and altitudinal distribution.* Abundant in most of the southern and midland counties, but becoming increasingly rare north of Shropshire, Derbyshire and Lincolnshire. It is also local and/or rare in several of the western counties, e.g. Devon, Cornwall and most of Wales, apart from the areas of Lias, Carboniferous Limestone and Old Red Sandstone in Brecon, Glamorgan and Monmouth, where it is often abundant; its distribution in the west is closely associated with that of calcareous soil. Exact northern limits of spontaneous occurrence doubtful; Baker & Tait (1868) regarded it as not indigenous north of the Tyne, and Hodgson (1898) says alien in Cumberland. Its status in Lancashire, north Yorkshire and Durham requires further study (cf. X). Baker (1863) records it from limestone scree woods in the Cleveland Hills, where it is presumably indigenous.

In Scotland local and rare and probably not indigenous. Lightfoot (*Flora Scotica*, 1778) says 'in woods but not very common' and gives three records, regarding one of which Sibbald (*Scotia Illustrata*, 1683) says 'Amongst the Plantings at Kinfawns' (Perth). Usually obviously planted in its Scotch stations, but there are a few records for it growing in woods as far north as Forfar (e.g. Queensferry, Woodforde, 1824; Mains of Hallerton, Gardiner, 1848).

For Ireland Druce (Comit. Fl.) follows Cyb. Hib., which says 'apparently native in some stations in Derry, Mayo and Antrim', but Stewart & Corry (1938) and Praeger (Bot. Irl., 1934) regard it as introduced in these stations and not indigenous anywhere in Ireland.

Northern limits in Europe: Durham—Denmark (absent from Bornholm)—south-west Schone in Sweden (rare)—Danzig—Grodno—Vladimir—Voronezh—Kharkov—Crimea—Turkestan. Southern limits: central Spain (common in Pyrenees, rare southwards to neighbourhood of Valentia)—Corsica (very rare)—Sicily—north Balkans—Asia Minor—Caucasus. Very rare in Algeria (cf. Barbey, 1934).

A lowland species, probably rare in Britain above 300 m. (1000 ft.). In north Yorkshire (Cleveland Hills) 274 m. (900 ft.) (Baker, 1863), in west Yorkshire, 186 m.

(600 ft.) (Lees, 1888), in Derbyshire 320 m. (1050 ft.) (Painter, 1889), in Brecon at Llanthony 380 m. (1250 ft.).

In Bavaria 750–800 m. (Hartig, 1851), in calcareous alpine foothills 750 m. (Hempel & Wilhelm, 1889), in Jura of Neuchâtel 1200 m., in south Switzerland 1400 m. (Hegi, Fl. **5**), in Caucasus 1800 m. (Elwes & Henry, 1906–13).

II. *Habitat.* Woods, hedgerows and scrub. In many districts (e.g. Monmouth apart from the limestone areas) (A. E. Wade), Anglesey, East Riding of Yorks and Cheshire (records in local floras), is mainly or exclusively a hedgerow species (cf. IV and X).

On the Continent in a very wide range of habitats varying from dry limestone slopes with southern aspect where it may be associated with *Quercus pubescens* Willd. (Hegi) to swamp woods in valley floors and to saline steppe soils (Dengler, 1930); it is characteristic of mixed broad-leaved woodland, especially with species of genera such as *Quercus*, *Tilia*, *Ulmus* and *Castanea*, and is rare in coniferous forest. Occasionally forms-stands, e.g. in the Oderwäldern at Brieg, Silesia (Hartig, 1851), but usually occurs as isolated trees or coppiced underwood.

On soils with a very wide range of texture, drainage conditions and base status, but with a very strong preference for those of high base status, and only abundant on such soils; probably never on podsols. As a hedgerow plant (where it may have been sometimes planted—cf. X) its range is considerably greater than as a woodland plant; thus it is present in hedges on the highly siliceous Bunter Pebble Beds of south Staffs, with pH 5·5–6·0, but in woodland it is probably absent on such low base status soils unless there is lime at depth. Thus on the Old Red Sandstone at Llanthony (Brecon) it is present on a degraded carbonate-free soil with acid reaction and very low exchangeable base content, but calcareous cornstones are present in the sandstone, and the accompanying vegetation includes many basicole species (cf. also stands 8, 9, p. 244). Salisbury & Tansley (1922) record it from woods on the non-calcareous Malvernian and May Hill Sandstones as well as from the Silurian limestones, but again it is associated with basicole species such as *Fraxinus*, *Cornus* and *Euonymus*. Horwood & Gainsborough (1933) record it from Coal Measures, Bunter Pebble Beds, Pennine Boulder Clay and peat as well as from the more calcareous clays and limestones, but not from the older igneous rocks, schists and shales of Charnwood Forest.

In a sample of 100 stands drawn from many districts in southern England and Wales in which *A. campestre* was present in either woodland or scrub, forty-three were on limestone or associated clays and drifts (including the Jurassic clays) thirty-six were on chalk or associated Clay-with-Flints, Chalky Boulder Clay, etc., eleven were on Old Red Sandstone, two were on Tertiary soils and two were on palaeozoic shales (both these on Wenlock Shales in localities where these are distinctly basic—cf. p. 225, stand 12). In the woods of Symonds Yat district in Monmouth and Gloucester from which I have approximately equal numbers of stands from Carboniferous Limestone, Coal Measures and Old Red Sandstone, I have twenty-seven records of *A. campestre* from limestone, eleven from Old Red Sandstone and none from Coal Measures. In south Wales it is common on the Carboniferous Limestone and Lias of Monmouth and Glamorgan, and on parts of the Old Red Sandstone, but nearly or quite absent elsewhere; in north Wales it is only recorded from limestone (H. A. Hyde). On Old Red Sandstone it is confined either to calcareous horizons or to fertile basic colluvial or alluvial valley-bottom soils, and the same is probably true of Tertiary soils (cf. stands 8, 9 and 10). It appears to be absent except as an occasional hedgerow plant from the Triassic sands of Stafford, Nottingham and Cheshire, the Greensand of Surrey, the Boulder Clays of Lancashire, and most Tertiary and Wealden clays.

The soils where it is present in woodland include shallow porous rendzinas on chalk, rendzinas and brown forest soils of high-base status on both deep and shallow tenacious clays, sandy loams of high-base status with drainage ranging from free to imperfect, heavy clays with gleying to within 15 cm. (6 in.) of the surface, and river gravel flats probably liable to inundation. Optimum conditions for abundance seem to be found on the heaviest limestone soils, e.g. heavy loams and clays over limestone.

III. *Communities.* The following will refer solely to occurrence in woodland and scrub.

A very characteristic member of the southern forms of ash and ash-oak wood. *Fraxinus*, *Ulmus glabra* (wych elm), *Corylus*, *Cornus* and *Crataegus monogyna* are very common and characteristic associates, though at times to be found in company with most British trees and shrubs. In a selection of eighty-three stands representing small areas the following were the principal trees and shrubs associated, with the percentage of stands in which present:

Acer campestre	100	Crataegus spp.	43
Fraxinus excelsior	64	Ilex aquifolium	27
Quercus spp.	55	Cornus sanguinea	20
Betula spp.	28	Sambucus nigra	19
Ulmus glabra	22	Euonymus europaeus	16
Fagus sylvatica	20	Ligustrum vulgare	14*
Prunus avium	16	Prunus spinosa	12*
Taxus baccata	10	Viburnum lantana	8
Tilia cordata	8	V. opulus	6†
Sorbus aria	6	Pyrus malus	4
S. aucuparia	5	Sarothamnus scoparius	1
Alnus glutinosa	1	Rhamnus cathartica	1
Corylus avellana	67	Salix atrocinerea	1

* On clay or limestone.

† On clay.

It is noteworthy that ash is a more frequent associate than oak. The relative scarcity of the photophilous basicole shrubs such as *Viburnum lantana* and *Rhamnus cathartica* is also striking.

By far the commonest dominant of the ground vegetation in stands where *A. campestre* is present is *Mercurialis perennis*, often with *Scilla non-scripta*, *Sanicula europaea*, *Asperula odorata* and similar woodland herbs, but on wetter sites *Allium ursinum*, *Filipendula ulmaria* or *Calamagrostis epigeios* may be present.

When young it is one of the most tolerant of the common basicole trees, enduring similar conditions of shade to *Corylus*, *Crataegus*, *Ulmus glabra* and *Ilex*, slightly deeper shade than *Cornus* and much deeper shade than *Viburnum lantana*. Wiesner (1907) gives the 'Lichtgenuss' as 1/43 (the relative light intensity at the point in the crown where foliage ceases—cf. Wiesner, p. 141). Thus it enters beech woods to some extent; Adamson (1922) records it as one of the most abundant shrubs of the Ditcham Park beech woods, and it is frequent in the beech woods on limestone north of Cardiff (H. A. Hyde). In the Chiltern beech woods it is usually either confined to small gaps or to woods where there is an unusually large admixture of other species such as *Fraxinus*, *Ulmus* and *Prunus avium* in the canopy. The Earl of Haddington (1733, p. 37) says: 'The dropping of its leaves is so pernicious, that no other tree can live below it, though the maple itself will thrive under everything.'

It may be present as a tree, as coppice, or as an uncoppiced shrub in the understorey.

(i) *As coppice.* Its commonest form; coppice conditions favour it because of its tolerance of shade and the great freedom with which it coppices. Its abundance in coppice woodlands doubtless depends largely on the care with which they have been tended, but some early writers recommend it for coppice; e.g. Marshall (1796) says, 'The principal value is for underwood; it is of quick growth and affords good fuel', and Haddington (1733, p. 28) says, 'Chestnut is the best underwood of any, the Maple only excepted'. Its volume production is, however, smaller than that of *Corylus* coppice (The. Hartig, 1851). On heavy limestone soils it is sometimes the principal component of the coppice. It reaches a much larger size than hazel, and will coppice well on a much longer rotation, e.g. 40–50 years, and consequently is often associated with coppice of *Ulmus glabra*, *Tilia cordata* and *Fraxinus*.

(ii) *As a tree.* Usually in rather poorly stocked open woodland where it has entered gaps, or has entered after the wood has been heavily cut over and then completely neglected. In such places it is often 12–15·5 m. (40–50 ft.) tall and may exceed in size standard oak growing with it. On Oolite in Bagley Wood, Oxford, it colonizes gaps in mixture with *Crataegus* and *Fraxinus*. Above Llanthony (Brecon) are a few isolated old trees in open Pteridietum amongst the scattered relict trees of woodland—oak, birch, holly, hawthorn, wych elm, yew and ash.

(iii) *As uncoppiced shrub in understorey of mixed deciduous woods.* Often juvenile or partially suppressed individuals only;—e.g. at Staunton, Glos (Forest of Dean) on Carboniferous Limestone in high forest of oak (*c.* 120 years) and ash (*c.* 70 years) was an understorey of *Crataegus monogyna* (o.-l.f.), *Corylus avellana* (a.), *Acer campestre* (small trees, f.), *Viburnum opulus* (r.), *Ulmus glabra* (v.r.), *Tilia cordata* (o.), while in gaps were saplings of *A. campestre*, *Tilia*, *Corylus*, *Cornus* and *Acer pseudo-platanus*.

Acer campestre is not a pioneer species in the invasion of grassland, etc., and is present in scrub only in the later seral stages. Thus, though abundant in neighbouring hedgerows and present in mature beech woods of the Chiltern escarpment, it is completely absent from developing scrub. In Watt's (1926) lists for the South Downs it is practically confined to the later stages (yew-ash and ash-oak) of the 'Yew with Ash' sere, which is apparently characteristic of the more sheltered sites (? and deeper soils).

It does not enter young plantations in the early stages, though it sometimes enters freely into broad-leaved plantations when they are beginning to form closed canopy; I have not recorded it from a coniferous plantation.

Dengler mentions *A. campestre* as characteristic of 'Auenwalder' (swamp woods), but it is not to my knowledge common in this type of wood in this country; stand no. 11, p. 244, is an example of occurrence in a wet situation, and Horwood & Gainsborough (1933) record it from woods of the alder-willow series.

Of the following stands for woodland with *A. campestre* 1–4 may be taken as typical of limestone, 5–7 of heavy basic clays, and 8–10 of soils of lower base status; for a further example on soil of low base status see *A. pseudo-platanus*, stand 12, p. 225. For examples on chalk the numerous lists of Adamson (1922) may be consulted.

Notes on species lists

(1) Kiddington, Oxon. Rendzina; *c.* 60 cm. (2 ft.), heavy loam over Oolite. Regularly cut coppice-with-standards woodland.

(2) Lower slopes of Wye Valley at Staunton, Glos. Brown forest soil, high-base status. 1–1·5 m. colluvial heavy loam over Carboniferous Limestone. 40-years coppice of very large stools of *Acer campestre* a., *Fraxinus* f., *Tilia cordata* o., *Fagus* o., *Betula* sp. f., with many poles of *Fraxinus* and *Betula*, and a few standards of *Quercus*, *Fraxinus* and *Fagus*.

(3) Ibid. Rendzina on tenacious clay over Carboniferous Limestone. Coppice of *Acer campestre* a., *Fraxinus* a., *Corylus* f., *Betula* spp. f. with many poles of *Fraxinus* and *Betula*, and a few standards of *Fagus*.

(4) Ibid. Shallow rendzina over Carboniferous Limestone; moist northern slopes. Coppice of *Acer campestre* a., *Corylus* a., *Ulmus glabra* a., and *Fagus sylvatica* f.

(5) Honeycomb Wood, Sherborne, Dorset. Rendzina on Forest Marble Clay. Irregular coppice with standards, poorly kept. Coppice mainly *Corylus*, but with frequent *Acer campestre*.

(6) Whitfield Wood, Dorset. On Oxford Clay.

(7) Composite list from Hell Coppice and Pole Cat End, two woods of very similar character, near Stanton St John, Oxford. On Oxford Clay. Soil gleyed to within 6 in. of surface. Oak standards with dense regular hazel coppice. Species marked † are mainly by ride sides.

(8) Reddings Inclosure, Staunton (Forest of Dean), Glos. Brown forest soil, low-base status, on deep colluvial sand derived from Old Red Sandstone Conglomerate. About 0·03 % exchangeable Ca. *Acer campestre* is very local on this soil, and is always associated with the equally local *Tilia*, *Fraxinus* and *Euphorbia amygdaloides*. High forest of oak.

(9) Ibid. Alluvium of Old Red Sandstone material. Very deep uniform finely mottled sandy loam, imperfectly drained, but probably only waterlogged for short periods. High forest of oak.

(10) Alluvium of river Blackwater at Poundhill, New Forest, Hants. Spontaneous woodland in which scrub, mainly of *Crataegus*, is being invaded by ash and oak. Note the presence of *Euphorbia amygdaloides*, and *Brachypodium sylvaticum*—local species in the New Forest woods which indicate a higher base status than usual.

(11) Alluvial gravel of Thames near Henley. Summer water-table at *c.* 60 cm. (2 ft.); liable to inundation. Oak standards over irregular coppice of large stools of ash and hazel which have not been cut for many years. Many uncoppiced shrubs, including *A. campestre*, in understorey. Species marked * are in dense shade, and species marked † in slight depressions.

	1	2	3	4	5	6	7	8	9	10	11
Fraxinus excelsior	v.a.	f.-a.	a.	f.	a.	.	f.	f.	r.	f.	a.
Quercus spp.	d.	o.	r.	o.	a.	a.	a.	d.	d.	f.	o.-f.
Betula spp.	.	f.	f.	.	.	.	l.	.	.	.	o.
Ulmus glabra	r.	.	.	a.	.	.	.	.	.	.	.
Tilia cordata	.	o.	.	.	.	.	.	.	o.	.	.
Prunus spinosa	.	.	.	.	.	f.	r.	.	.	.	.
P. avium	r.	.	.	.	.	.	.	.	.	.	.
Populus tremula	.	.	.	.	.	.	l.a.	.	.	.	.
Ulmus procera	.	.	.	.	.	.	.	.	.	.	f.
Acer campestre	v.a.	a.	a.	a.	.	.	o.-f.	r.	r.	o.	o.
Corylus avellana	a.	f	f.	a.	.	d.	d.	a.	f.	.	l.
Crataegus spp.	r.	r.	r.	o.	.	.	f.	.	.	v.a.	.
Cornus sanguinea	v.r.	.	o.	.	.	.	f.	.	.	.	r.
Ligustrum vulgare	l.o.	.	.	.	l.v.a.	f.	o†	.	.	.	.
Viburnum opulus	.	.	.	.	f.-a.	.	o.	.	.	.	o.
Euonymus europaeus	.	.	o.	.	.	.	.	.	r.	.	.
Salix atrocinerea	.	.	.	.	.	.	f.	.	.	.	f.
Taxus baccata	.	.	r.	.	.	.	.	.	.	a.	.
Sambucus nigra	l.f.	.	.	.	.	.	.	.	.	.	f.
Rhamnus cathartica	.	.	.	.	.	.	.	.	.	.	r.
Rubus fruticosus	.	v.a.-l.d.	.	f.	f.	.	f.†	d.	d.	l.d.	r.
Mercurialis perennis	d.	.	l.d.	f.-v.a.	.	.	.	.	a.-l.d.	.	.
Pteridium aquilinum	.	.	.	.	d.	.	.	r.	l.a.	.	.
Allium ursinum	.	.	.	d.	.	.	.	.	.	.	.
Ajuga reptans	v.r.	.	.	.	f.	v.a.	o.	.	.	a.	.
Carex sylvatica	.	o.	r.	.	f.	r.	r.	.	.	.	.
Deschampsia caespitosa	.	r.-f.	r.	.	.	.	l.†	o.	o.	.	.
Euphorbia amygdaloides	.	.	v.r.	.	f.	.	o.	o.	.	r.	.
Primula vulgaris	e.l.	.	r.	.	f.	f.	l.	.	.	.	.
Viola riviniana?	.	r.	o.	.	.	v.a.	r.	.	.	f.	.
Hedera helix	.	v.a.-l.d.	f.	f.	.	.	.	v.a.	v.a.	.	.
Scilla non-scripta	e.l.	o.-l.a.	l.f.	l.	.	.	.	.	.	.	.
Lonicera periclymenum	.	.	.	.	o.	a.	r.-l.a.	.	.	.	.
Urtica dioica	v.r.	.	.	.	.	.	.	.	f.	.	d.*
Luzula pilosa	.	r.	.	.	.	f.	f.-a.	.	.	.	.
Geum urbanum	.	.	.	.	.	.	o.	.	v.r.	.	r.
Milium effusum	.	.	.	.	.	r.	r.	o.	.	.	.
Potentilla sterilis	.	.	.	.	.	o.	o.	.	.	f.	.
Filipendula ulmaria	.	.	.	.	r.	r.	.	.	.	.	l.c.d.†
Agrostis spp.	.	.	.	.	.	.	.	.	.	a.	l.f.-c.d.†
Asperula odorata	.	.	.	.	f.	.	.	o.	.	.	.
Arenaria trinervia	.	.	.	.	.	.	.	.	.	f.	f.*

	1	2	3	4	5	6	7	8	9	10	11
Arum maculatum	r.	.	.	.	.	.	.	.	o.	.	.
Epilobium montanum	.	.	.	.	f.	.	l.f.	.	.	.	.
Lamium galeobdolon	.	.	r.	.	.	.	.	a.	.	.	.
Brachypodium sylvaticum	.	.	.	.	.	.	l.†	.	.	f.	.
Rosa spp.	.	.	.	.	.	.	r.-f.†	.	.	r.	.
Rubus caesius	.	.	.	.	.	.	f.	.	.	.	o.
Rumex sanguineus var. viridis	.	.	.	.	.	o.	.	.	.	.	o.
Daphne laureola	.	.	r.	.	.	.	.	.	.	.	.
Anemone nemorosa	.	.	.	r.	.	.	.	.	.	.	.
Circaea lutetiana	.	.	.	.	a.-v.a.	.	.	.	.	.	.
Fragaria vesca	.	.	.	.	a.	.	.	.	.	.	.
Galium palustre	.	.	.	.	r.	.	.	.	.	.	.
Listera ovata	.	.	.	.	r.	.	.	.	.	.	.
Habenaria chlorantha	.	.	.	.	.	r.	.	.	.	.	.
Poa nemoralis	.	.	.	.	.	.	l.	.	.	.	.
Chrysosplenium oppositifolium	.	.	.	.	.	.	.		o.	.	.
Stellaria uliginosa	.	.	.	.	.	.	.	.	.	o.	.
Symphytum officinale	.	.	.	.	.	.	.	.	.	.	l.a.-c.d.†
Cirsium palustre	.	.	.	.	.	.	.	.	.	.	l.f.†
Carex remota	.	.	.	.	.	.	.	.	.	.	r.
Festuca gigantea	.	.	.	.	.	.	.	.	.	.	r.
Humulus lupulus	.	.	.	.	.	.	.	.	.	.	r.
Ranunculus repens	.	.	.	.	.	.	.	.	.	.	l.f.†
Solanum dulcamara	.	.	.	.	.	.	.	.	.	.	r.
Dryopteris filix-mas	v.r.	o.	.	o.	.	r.	.	o.	o.	.	.
Polystichum aculeatum var. lobatum	.	.	r.	.	.	.	.	.	.	.	.
P. aculeatum	.	.	.	o.	.	.	.	.	.	.	.
Scolopendrium vulgare	.	.	.	a.-v.a.	.	.	.	.	.	.	.
Thuidium tamariscinum	a.	f.	.	.	f.	f.	v.a.	Bryophytes not listed; nearly absent	.	f.	.
Eurhynchium striatum	f.	.	Bryophytes not listed	f.	f.	.	v.a.		.	.	.
E. piliferum	f.	r.		o.	.	.	.		.	.	.
E. praelongum	a.	.		o.	.	.	l.a.		.	.	.
Mnium undulatum	f.	f.		o.	f.	.	.		.	.	.
Catharinea undulata	.	r.		.	.	f.	l.a.		.	.	.
Hylocomium triquetrum	.	v.a.		.	.	f.	l.a.		.	.	.
Brachythecium rutabulum	o.	r.		.	.	.	.		.	.	.
Fissidens taxifolius	.	f.		.	.	.	.		r.	.	.
Porotrichum alopecurum	.	.		v.a.	.	.			.	.	.
Hylocomium brevirostre	v.r.	.		.	.	.	.		.	.	.

IV. *Response to biotic factors.* Coppices very freely up to an age of 60–100 years. Very tolerant of cutting and grazing of shoots; this, together with powers of coppicing, adapts it well for hedges. Feeble suckers are occasionally formed but are of no importance as a means of propagation.

V. (*a*) *Gregariousness.* See III.

(*b*) *Performance.* Usually attains a height of 9–15 m. (30–50 ft.); the maximum recorded height in Britain seems to be 76 ft. (23·2 m.) (Elwes & Henry, 1906–13). Records of performance and of height and diameter growth are summarized in Fig. 2. Diameter increment is slow after the first 20 years. A tree in Bagley Wood, Oxford, with a diameter at breast height of about 35 cm. (14 in.) was about 80 years old, and one near it with a diameter at breast height of 41 cm. (16 in.) about 120–130 years old. Hegi states that 3·3 m. girth is the maximum; Loudon (1838) records a cultivated tree at Stirling which was 4 ft. diameter.

For amounts of foliage and fruit on a tree, see Tables, p. 231.

(*c*) *Effect of frost, drought, etc.* Not liable to damage by frost in this country, nor apparently on the Continent (Hempel & Wilhelm, 1889). Often in situations where it must tolerate considerable drought (cf. II, association with *Quercus pubescens*). In spring of both 1942 and 1943 trees in exposed situations suffered much damage from high winds in May when young leaves and shoots were very tender.

VI. *Morphology.* (*a*), (*b*) *Roots.* An old tree on deep colluvial calcareous loam with water-table at 13–16 dm. (4–5 ft.) was examined in December 1943. Skeletal root system relatively deep, consisting of roots descending obliquely from the stock; vertically descending 'sinkers' scarcely differentiated. Fibrous roots very abundant in upper 30 cm. (12 in.); frequent below throughout the whole depth of yellow soil, and a few present in the grey portions of the gleyed zone, but completely absent from uniformly blue-grey soil immediately above the water-table. Fibrous roots of upper 30 cm. richly and irregularly branched, 0·5–1·0 mm. diam., pale whitish colour, with little differentiation between branches of successive orders. Deeper roots clear reddish brown, with sharp differentiation between elongate little-branched axes and very slender short lateral branch systems. Root hairs few on mycorrhizal roots, abundant on non-mycorrhizal roots; slight indications of recent growth. Skeletal roots reddish brown with transversely elongated lenticels. On 6–7-year-old plants the tap root is weakly developed.

(*c*) *Mycorrhiza.* Endotrophic mycorrhiza of the Phycomycete type present, but sometimes only locally, in the upper roots. There is infection through the whole depth of the cortex; active hyphae and various digestion stages are present; very few vesicles and no arbuscules were seen in spring or summer, but they were abundant in winter. The deeper roots are non-mycorrhizal. (Material from Bagley Wood, Oxford, from a variety of soils, mainly rendzinas, examined by Dr I. Levisohn.)

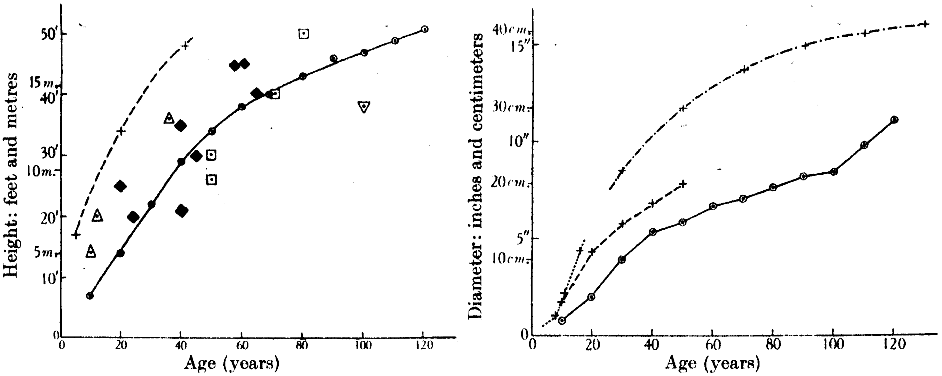


Fig. 2. Height and diameter growth of *Acer campestre*.

△ Scotland; ⊡ South-eastern England; ▽ Western England; ◆ Foreign; records from Loudon (1838). —·—+—·— Bagley Wood, Oxford, growth from 1842–1942 of a stem which is 41 cm. diameter at breast height. ··+··· Bagley Wood, growth of a sapling *c.* 20 years old growing near to above. ——+—— Bagley Wood, coppice stems on same soil. —⊙— Hartig (1851), on Muschelkalk, in same locality as corresponding curves for *A. pseudo-platanus* and *A. platanoides*, but on shallower soil.

Morphology of aerial parts. Growing in the open often forms a broad spreading crown. In closed stand often retains a main trunk to the apex, with slender lateral branches. The branches are brittle. See also introduction to *Acer*, pp. 215–16.

(*d*) *Perennation.* Mesophanerophyte with bud covering.

(*e*) *Vegetative reproduction.* See IV.

(*f*) *Longevity.* Hegi says to 200 years in the open, but it probably often attains this age. Loudon (1838) mentions a tree 4 ft. diam., 55 ft. high (1·2 and 16·5 m.) and 302 years old at Blairlogie, Stirlingshire. The hollow stump of the Boldre Maple in the New Forest is still alive, and is at present 213 cm. girth, 68 cm. diam. (84 and 26·8 in.); it was this size in Gilpin's time (*c.* 1800), and then can hardly have been less than 150 years old. Trees in Bagley Wood such as those mentioned in V (*b*) are still perfectly sound and thriving.

(*g*) *Age of plant at time of first flowering.* Hempel & Wilhelm (1889) say 25 years. But a small tree growing in shade in Bagley Wood is fruiting at 16–20 years of age. Coppice stems fruit at an age of 10 or less.

(*h*) *Seed production.* Probably some seed is produced by some trees in most years, but good seed years are sporadic (cf. VIII and IX). 1942 was a poor seed year over an area extending at least from Shropshire to Bucks and Hants; in populations around Oxford 50 % of the trees had no fruit and a further 25 % had very few. In the same populations in 1943, 90–100 % of the trees were fruiting, the majority heavily. No information is available regarding production of flower and fruit near its northern or altitudinal limits. Crump & Crossland in the *Flora of Halifax* (1904) say that it rarely flowers in that district. Mathieu (1897) says that seed production is abundant and regular (presumably in France).

(*i*) *Ecotypes.* No ecotypes are suspected. There appear to be no habitat differences between var. *hebecarpum* and var. *leiocarpum*; in England most populations contain a small proportion of the latter.

(*j*) *Chromosome number.* $n=13$ (basic number for genus). Pollen sterility 1–3 %. Reduction division very early, when flower buds are extremely small (Foster, 1933).

VII. *Phenology.* (*a*) Growth of roots, no information.

(*b*) Leaves appear in third to fourth week of April in Oxford district. The elongation of young shoot is completed by midsummer. Occasionally a few lammas shoots are formed; in 1943 these were being formed at the end of June.

(*c*) Flowers open about first week of May, but there is much variation amongst adjacent trees. Flowering period extends over nearly a month.

(*d*) Seed ripe in late September or early October; falls gradually from October onwards, a few in sheltered places remaining on tree throughout the winter. Much unsound fruit falls in September, 2–3 weeks before fall of sound fruit begins.

(*e*) Seedlings appear above ground about the first week of May. At Oxford in 1943 seed sown the previous autumn germinated between 2 and 5 May; in 1944 seedlings from the same sowing which had lain in the ground 18 months appeared *c.* 20 April.

VIII. *Biology of flower, fruit and seedling.* It is doubtful whether completely male trees exist; in 1942 in populations around Oxford only male flowers could be found on about 50 % of the trees, but in 1943 the proportion of male flowers was much smaller, and individuals fruited heavily on which thorough search in the previous year had revealed only male flowers. The same trees again produced a high proportion of male flowers in 1944.

Wittrock (1886) in populations near Budapest found the following proportions of trees with various types of inflorescence:

A	Entirely female, none	
B_1	Terminal flowers of inflorescence female, majority of lateral flowers also female	4 %
B_2	As B_1, but majority of lateral flowers male	42 %
B_3	As in B_2 but with some entirely male inflorescences	6 %
C	Terminal flowers of inflorescence male; laterals mixed, majority male	6 %
D_1	As C but majority of lateral flowers female	16 %
D_2	As D_1 but with some entirely male inflorescences	12 %
E	Entirely male	10 %
	Individuals with inflorescences of types B_2 and C mixed	4 %

Populations around Oxford in 1943 agreed with the above in so far as the most numerous class of tree is that with terminal flowers of inflorescence female and majority of lateral flowers male.

Mode of pollination: insect visitors. Flowers not scented but producing nectar, and visited, but not very energetically, by small bees (*Andrena* and *Halictus* spp.), by Syrphids and other Diptera and by Coleoptera (cf. lists on p. 219).

Hybrids. A hybrid with *A. opalus* Miller recorded from Continent (Schinz & Keller, 1923).

Amount and weight of seed. For amounts of seed per tree, see Table 2, p. 231. There are 5–20 flowers per inflorescence, and usually 2–5, but occasionally up to 12 fruit (each of two seeds). There is much variation in size of fruit. Average weight of samara, with wings, in one sample 0·074 g., in another 0·056 g.; average weight of embryos only in the second sample, 0·025 g. Rafn (1915) gives the range as 0·0698–0·0865 g., mean 0·0808 g. (There is an error in Salisbury's quotation of this figure in Rep. Capac.)

(*h*) *Dispersal.* By wind. Ridley (Disp. plts) gives 90 yd. (81 m.) as the maximum distance of dispersal from trees 20 ft. (6 m.) high in 'a tolerably strong breeze'.

(*i*) *Viability.* Only a small number germinate in the first spring after ripening (5–10 % in my own sowings of 1942–3), the rest remaining dormant till the following spring. This is in agreement with the majority of the statements in the literature. Impossible to give precise figures for viability owing to slowness and irregularity of germination, but certainly often low. Rafn (1915) gives the average viability as 70·9 %, ranging from 68 to 72 %, with no germination in first season. In eight samples of seed from Oxfordshire, Berkshire and Shropshire collected in 1942 the percentage of viable seed as judged from appearance of embryo ranged from 11 to 60 %, the average being 40 %. Usually 10–20 % were insect-infested, 14–26 % (but 73 % in one sample) empty and up to 44 % with shrivelled embryos. In 1943 with far heavier seed crops 60–86 % (average 74 %) were apparently sound, insect infestation being slight (7·5 % maximum), 10–16 % empty and 6–10 % with shrivelled embryos.

Other features of seed. The seed forms a striking contrast in character to that of *A. pseudo-platanus.* The embryo is very much smaller and more delicate, the endocarp is thick and stony, and the hairy lining of *A. pseudo-platanus* absent. Mice neglect empty *A. pseudo-platanus* fruit, but they usually open empty *A. campestre* fruit.

Morphology and biology of seedlings. The seedling is similar to that of *A. pseudoplatanus* but smaller, with thinner, rather more ovate cotyledons, *c.* 1·8–3·0 × 0·5–0·75 cm. The first foliage leaves are cordate-lanceolate to cordate-ovate, unlobed and scarcely dentate (cf. Fig. 3)*. Seedlings seem to be rather uncommon and of sporadic occurrence, partly doubtless as a result of irregular fruiting. H. A. Hyde reports having found them in abundance in south Wales in 1936 and 1941, and in Bagley Wood, Oxford, they were frequent in 1941 and there were a few in 1944 from the heavy seed crop of 1943, but none were seen in intermediate years. With one exception the few examples of young regeneration which I have seen have been in considerable shade on the woodland floor with little ground vegetation. In one locality saplings a few years old were abundant in thin turf at the edge of a wood beneath the shelter of overhanging beech branches; with them were young *Crataegus*, *Corylus*, *Quercus* and *Fraxinus*. The young plant stands considerable shade (though Mathey (1924) states that the seedlings need abundant light for survival) and probably usually find suitable conditions for establishment in or around small gaps, beneath canopy near rides, etc. The shelter of young coppice probably provides very suitable conditions. In one example on Oolite, saplings up to 2 ft. (0·6 m.) tall were growing and apparently thriving beneath beech, together with *Mercurialis perennis*, *Sanicula europaea*, *Anemone nemorosa*, etc., forming 50 % phanerogam cover with 50 % litter.

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* Cultivated seedlings at the end of their first year were 4·5–7·0 (mean 5·9) cm. tall.

IX. (*a*)–(*c*) *Parasites and diseases.* See the lists of insects and fungi in the introductory notes on pp. 216–18. None of the fungal or insect parasites appear to cause serious diseases.

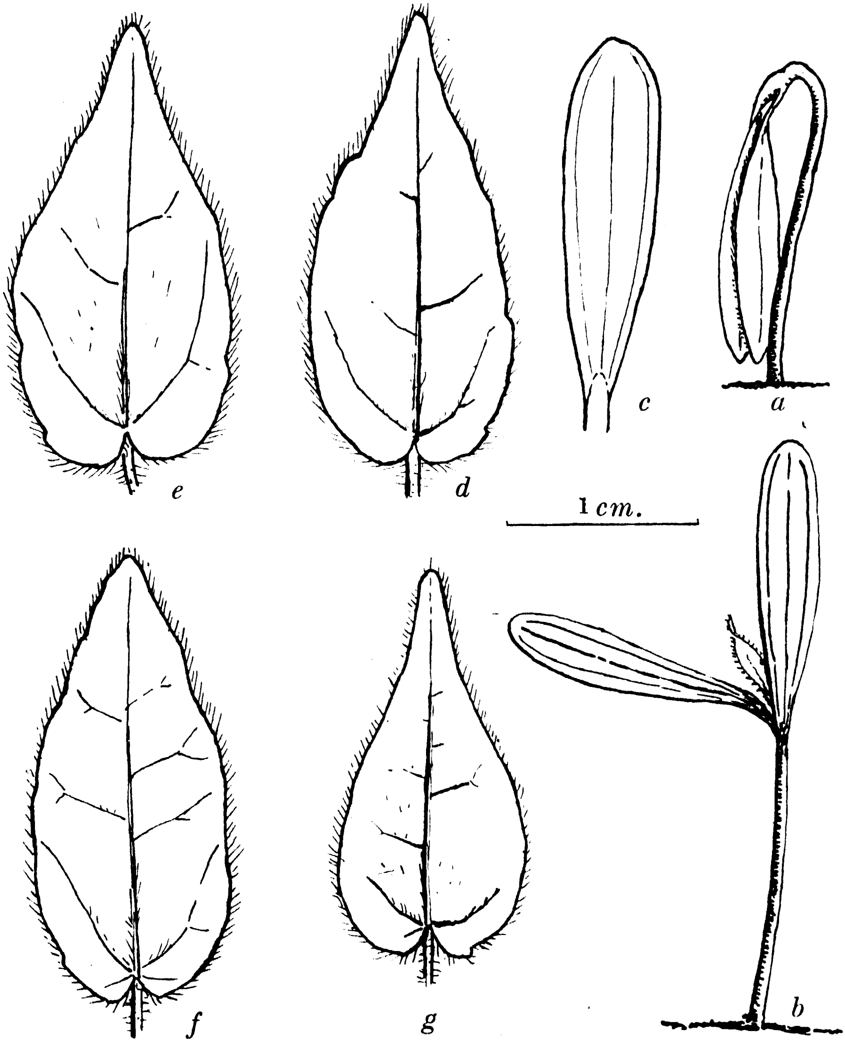

Fig. 3. (*a*) and (*b*) Successive stages in growth of young seedling. (*c*) Cotyledon. (*d*)–(*g*) First foliage leaves.

Aphids are almost always abundant, especially on the inflorescence. Mice eat the seeds readily, and snails devour seedlings. *Viscum album* has been recorded (Loudon, 1838) on the branches.

X. *History.* The Tertiary distribution of *Acer* section *Campestria*, was apparently the same as the modern distribution (Pax, 1902). *A. campestre* has been recorded from the

Cromer Forest Bed at Pakefield, Suffolk, and also from postglacial beds at Crossness, Essex (Clement Reid, 1899), and it is also known from preglacial and interglacial deposits in Jutland, Schone in Sweden, Thuringia, France, etc. (Jessen & Milthers, 1928; Schulz, 1900: Hegi, Fl. **5**; Pax, 1902).

The name maple is of Anglo-Saxon origin, and is of frequent occurrence in place-names in midland and southern counties; Ekwall (1936) records none north of Notts and Derby. The early herbalists all record it as being common. For its status in northern Britain and Ireland cf. I (*a*).

Loudon (1838) says that 'it is much used in France for forming hedges'; it may perhaps have formerly had extensive employment for this purpose in England, though the only specific references to this which I have been able to trace in early literature are by the Earl of Haddington (1733), who says, with reference to the Windsor forest district, 'They have ditches as usual, and plant the hedge with white thorn mixt with maple, crabs, hazel, alders, oak, ash and elm' (p. 66), and again 'the maple grows fast and under the drop of other trees, is a strong hedge, and makes good stakes and burnwood' (p. 69). On p. 37 he says 'It makes a pretty hedge in a wilderness'. It is still occasionally planted, probably mainly in hedges; a large firm of nurserymen inform me that they supplied three orders for this purpose during a five-year period. Hegi (Fl. **5**) says that it is planted for fodder in the Jura and Southern Alps.

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Sonchus asper (L.) Hill and *S. oleraceus* L., emend. Hill, R. A. Lewin, c/o The Botany School, Cambridge.

S. palustris L., Francis Rose, The Forge House, East Malling, Kent.

Spiranthes stricta Nels., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

Stellaria nemorum L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Subularia aquatica L., Dr N. Woodhead, Department of Botany, Bangor.

Suaeda fruticosa (L.) Forsk., and *S. maritima* (L.) Dum., Dr V. J. Chapman, Botany School, Cambridge.

Thlaspi alpestre L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

Tilia cordata Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.

Trientalis europaeus L., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

Ulmus spp., Dr R. Melville, The Herbarium, Royal Botanic Gardens, Kew.

Urtica spp., P. Greig-Smith, c/o The Botany School, Cambridge.

Vaccinium vitis-idaea L., P. A. Tallentire, 14 Hulme Hall Avenue, Cheadle Hulme, Cheshire.

Valeriana officinalis L. and *V. sambucifolia* Mikan, J. Carpenter, c/o The Botany School, Cambridge.

Viburnum lantana L. and *V. opulus* L., Dr H. Godwin, The Botany School, Cambridge.

Viola lutea Huds. and *V. tricolor* L., Dr P. E. Fothergill, King's College, Newcastle-on-Tyne.

Wahlenbergia hederacea Reichb., Francis Rose, The Forge House, East Malling, Kent.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account singly or in collaboration should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

Accounts ready for publication should be sent to Dr P. W. Richards, Botany School, Cambridge.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1943

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and *less* Payments in advance:						
Members taking *Journal of Ecology* only	217	10	0			
Members taking *Journal of Animal Ecology* only ...	127	7	3			
Members taking both Journals	96	15	0	441	12	3
Interest on Investments	55	2	1			
Interest on Deposit Account	2	2	11	57	5	0
Journal of Ecology. Sales less Cost				76	9	1
Index to *Journal of Ecology*, vols. I–XX, Sales ...	3	16	0			
Less Expenses	3	7	6		8	6
				575	14	10
Balance—Deficit for the Year (To Balance Sheet) ...				12	13	11
				£588	8	9
Journal of Ecology, 1943:						
Sales: Current vol. 31				441	14	0
Back volumes and parts				133	13	9
				£575	7	9
Journal of Animal Ecology, 1943:						
Sales: Current vol. 12				211	13	2
Back volumes and parts				50	8	4
Reprints of papers				10	15	6
				272	17	0
Balance (see above, under Expenditure)				405	0	7
				£677	17	7

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing and Stationery	3	5	10			
Postages	11	15	9			
Travelling	13	9	11			
Committee on Nature Reserves	43	7	2			
Meeting Expenses	17	12	0			
Audit Fee	3	3	0			
Bank Charges		10	5			
Clerical assistance	15	0	0	108	4	1
Grant: to Freshwater Biological Association ...				10	0	0
Biological Flora of the British Isles:						
Cost of Printing	80	7	11			
Less Sales	15	3	10	65	4	1
Journal of Animal Ecology. Cost *less* Sales				405	0	7
				£588	8	9
Journal of Ecology, 1943:						
Costs: Paper, Blocks, Printing and Binding ...				386	18	10
Publishers' Commission				82	11	9
Carriage, etc....				16	7	1
Insurance of Stock				6	10	0
Editorial expenses				6	11	0
				498	18	8
Balance (see above, under Income) ...				76	9	1
				£575	7	9
Journal of Animal Ecology, 1943:						
Costs: Paper, Blocks, Printing and Binding ...				602	14	1
Publishers' Commission				43	6	2
Carriage, etc....				10	19	8
Insurance of Stock				10	7	2
Fee for checking references				10	0	0
Special notice					10	6
				£677	17	7

BALANCE SHEET AT 31 DECEMBER 1943

Assets

	£	s.	d.	£	s.	d.
Cash at Bank: Current Account	158	18	0			
Deposit Account	350	0	0			
				508	18	0
Publishing Accounts—Amounts due from Cambridge University Press:						
Journal of Ecology. Balance of Account	272	16	5			
Journal of Animal Ecology. Balance of Account...	106	19	6			
Journal of Ecology. Index Volume		8	6			
Biological Flora of the British Isles...	12	3	3			
				392	7	8
Investments at Cost:						
Held 31 December 1942—						
£1,200 of 3½% War Loan	1,230	4	1			
£200 of 5% Conversion Loan	198	10	0			
Purchased 28 April 1943—						
£300 of 3% Savings Bonds	300	0	0			
				1,728	14	1
				£2,629	19	9

A further Asset, not valued, is the Unsold Stock of Journals and Index Volume held by the Publisher for the Society.

VICTOR S. SUMMERHAYES,
ALEX. S. WATT.
Hon. Treasurers.

Liabilities

	£	s.	d.	£	s.	d.
Members' Subscriptions, prepaid for 1944				9	15	0
Library Fund				1	5	0
Grant from F. L. Vanderplank for *Journal of Animal Ecology*				5	0	0
Printing Accounts due to the Cambridge University Press:						
Journal of Ecology, vol. 31, no. 2 and Reprints ...	229	19	9			
Journal of Animal Ecology, vol. 12, no. 2 and Reprints	392	2	10			
				622	2	7
Sundry Accounts due:						
Nature Conservation Report (two Accounts) ...	31	2	6			
Expenses of Special Meeting	2	5	0			
				33	7	6
General Revenue Account:						
Surplus in hand 31 December 1942	1,971	3	7			
Less Deficit for 1943...	12	13	11			
				1,958	9	8
				£2,629	19	9

Audited and found correct, and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS
Chartered Accountants.

120 Bishopsgate, E.C. 2
and
231*a* High Road, Loughton, Essex.
9 *May* 1944.

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